Chapter 6

THE ANIMAL COMMUNITY: DIVERSITY AND RESOURCES

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INTRODUCTION

The fauna of deciduous forests is diverse, ranging from Protozoa to large mammals. Their biotic activities are manifold and their spatial and temporal distribution is complex. The forest habitat consists of a heterogeneous patchwork of different soil structures, vegetation textures and abiotic factors such as light and moisture. Additionally temperate deciduous forests are characterized by a strong seasonality in climate, structure and availability of resources.

This complexity greatly hampers analysis of the structure and function of the forest fauna. Hence studies on the animal community of temperate deciduous forests are largely in the descriptive phase. Separate components of the forest ecosystem have been studied extensively, but few attempts have been made to synthesize the data.

In my analysis I have distilled principles from the large number of detailed studies on temperate deciduous forests, and have emphasized the interrelationships between populations of animals, micro-organisms and higher plants. I have concentrated on illustrative examples from a diverse range of forest habitats. The treatment emphasizes general concepts, and is not intended to be a comprehensive review of the structure and function of the fauna.

In this chapter I will focus on distribution, temporal patterns, trophic relationships, diversity and resource partitioning of the animal groups. I often refer to my own studies in a mull beech-wood on limestone (Göttinger Wald, West Germany), because I am familiar with this ecosystem. The role of animals in energy flow and nutrient cycling is analysed in Chapter 9.

COMPOSITION OF THE FAUNA

Protozoa, nematodes, oligochaetes, mites (Acarina), springtails (Collembola) and dipterous larvae dominate in the soil. In the litter layer mites, springtails, other arthropods (spiders [Araneida], centipedes [Chilopoda], millipedes [Diplopoda], isopods and beetles [Coleoptera]) and snails are abundant (some of them only in mull forests). Hemiptera, phytophagous Coleoptera, Hymenoptera and Lepidoptera are typical for the vegetation layers. Some basic patterns are summarized in Table 6.1. Important summaries of the biology of soil and litter animals are those of Müller (1965), Burges and Raw (1967), Brauns (1968), Wallwork (1970, 1976), Dickinson and Pugh (1974), Petersen and Luxton (1982) and Dunger (1983). The fauna of the soil and vegetation layers has been introduced by Elton (1966) and Packham and Harding (1982). Morris and Perring (1974) have given a detailed account of the fauna of British oak forests. The vertebrate fauna is treated by Duffey (1980), by Rahmann (1986) for Central European forests and by Kitchings and Walton (Chapter 11, this volume) for forests in North America.

Micro-organisms, in addition to animals, are important heterotrophs in deciduous forests. Accounts of the microflora — bacteria, actinomycetes and fungi — in temperate deciduous forests have been given, among others, by Burges and Raw (1967), Dickinson and Pugh (1974), Szabó (1974), Swift et al. (1979), and Kjoller and Struwe (1982).

TABLE 6.1

Synopsis of invertebrate animal groups characteristic of temperate deciduous forests. Data apply to mull and/or moder (mor) soils. Parasites of invertebrates are not included

Animal group	Size class[a]	Preferred stratum[b]			Number of species[c]	Density biomass[c]	Nutritional type[d]	Some recent references[e]
Protozoa								
Flagellata	mi	s	l	a	−	−/−	sa (fluids)	
Rhizopoda	mi	s	l	a	+	+/+	mi	Meisterfeld (1980); Lousier (1982)
Ciliata	mi	s	l	a	−	−/−	mi	
Turbellaria	mi	s		a	−	−/−	zo	
Rotatoria	mi	s		a	−	−/−	mi sa zo	
Nematoda	mi	s	v	a	+	+/+	ph mi sa zo	Phillipson et al. (1977); Popovici (1984)
Mollusca								
Gastropoda	ma	l	v(s)		+	+/+	ph sa (zo)	Corsmann (1981); Phillipson (1983); Phillipson and Abel (1983)
Annelida								
Enchytraeidae	me	s(l)			+	+/+	sa mi	Phillipson et al. (1979)
Lumbricidae	ma	s(l)			−	+/+	sa mi	Phillipson et al. (1978); Satchell (1983); Zicsi (1983)
Tardigrada	mi	s		a	−	+/+	mi zo	Hallas and Yeates (1972)
Arachnida								
Araneida	ma	l	v		+	−/−	zo	Albert (1982); Stippich (1986)
Pseudoscorpionida	ma	l(v)			−	−/−	zo	Goddard (1976)
Opilionida	ma	l	v		−	−/−	zo	Bachmann and Schaefer (1983); Schaefer (1986)
Acari								
Mesostigmata	me	s	l		+	−/−	zo sa mi	Luxton (1982); Athias-Binche (1983)
Prostigmata	me	s	l	v	−	−/−	zo mi sa ph	Luxton (1981g)
Astigmata	me	s	l		−	−/−	mi	Luxton (1981f)
Cryptostigmata	me	s	l		−	+/+	sa mi	Luxton (1972, 1975, 1981a–e)
Crustacea								
Harpacticoida	mi	s		a	−	−/−	mi (sa)	
Isopoda	ma	l			−	+/+	sa mi	
Myriapoda								
Chilopoda	ma	l	s		−	+/+	zo	Albert (1980)
Diplopoda	ma	l			−	+/+	sa mi	Sprengel (1986)
Pauropoda	me	s			−	−/−	sa mi	
Symphyla	me	s			−	−/−	mi ph	
Hexapoda (Insecta)								
Diplura	me	s			−	−/−	mi sa zo	
Protura	me	s			−	−/−	mi sa	
Collembola	me	s	l	v	+	+/+	mi sa	Wolters (1983, 1985)
Blattariae	ma	l	v		−	−/−	sa pa	
Dermaptera	ma	l	v		−	−/−	pa	
Ensifera	ma	v	l		−	−/−	zo ph	
Psocoptera	me	v			−	−/−	mi	
Thysanoptera	me	v			−	+/−	ph zo	
Hemiptera	ma, me	v			+	+/+	ph zo	
Planipennia	ma	v			−	−/−	zo	Nielsen (1977)
Coleoptera	ma	l	v		+	+/+	zo ph	Friebe (1983); Schaefer (1983a)
Hymenoptera	ma, me	v	l		+	+/+	zo ph	Ulrich (1987)
Lepidoptera	ma	v			+	+/+	ph	Winter (1985)
Trichoptera	ma	l			−	−/−	sa	
Diptera	me, ma	s			+	+/+	sa mi ph zo	Hövemeyer (1984, 1985)

[a]mi = microfauna, me = mesofauna, ma = macrofauna, meg = megafauna.
[b]s = soil, l = litter, v = vegetation, a = semiaquatic.
[c]+ = high, − = low.
[d]sa = saprophagous, mi = microphytophagous, ph = phytophagous, zo = zoophagous, pa = pantophagous.
[e]Additional reference for most of the groups Ellenberg et al. (1986).

THE HABITAT AND THE FAUNA: PATTERNS OF OCCURRENCE, DISTRIBUTION AND SPATIAL DYNAMICS

The complex horizontal and vertical structure of forests makes arbitrary any method of classifying forest subsystems. Swift et al. (1979) distinguished three functional subsystems: the plant subsystem, the herbivore subsystem (which is closely linked to it), and the decomposition subsystem. These units are closely interrelated, making it difficult to separate clearly the components of a forest. For practical purposes I have differentiated between the soil–litter system and the above-ground plant system, as is done by Mattson (1977). The borderline between these two distinct subunits is the interface separating the ground zone and the field layer (cf. Elton, 1966), this being a boundary for most animal populations. One of the reasons why the soil–litter system and the above-ground plant system are so different is the contrasting microclimate. However, more important is the fact that the food source of many animal populations lies either in the canopy layer, the herb layer or on the forest floor.

The soil–litter subsystem

In the soil the lithosphere, atmosphere and biosphere are interwoven. Microhabitats of animals are the pore spaces filled with air or water, the water film on the surface of soil particles, plant remains, tunnels and burrows constructed by the animals themselves. The litter layer is a voluminous system of interstices filled with air and inhabited by animals. Both strata are difficult to describe in relation to the fauna because the attributes of the environment depend on the size of the organisms, reaching from the microsites of soil amoebae to the home range of forest mammals.

On one scale the forest floor is a relatively stable and predictable habitat, since daily and even annual fluctuations in the physical environment are comparatively small. On the other hand the most characteristic feature of the soil and litter environment is its vertical stratification in abiotic factors such as moisture, temperature, concentration of oxygen or carbon dioxide, and content of organic matter (Wallwork, 1976), paralleled by a stratification in the biotic environment — that is, food quality and pressure by enemies.

Horizontal distribution

Aggregation and patchy distribution. Soil and litter invertebrate populations are usually non-randomly dispersed, often appearing to have an aggregated dispersion pattern (Joosse, 1970; Reise and Weidemann, 1975; Usher, 1976; Usher et al., 1982; Petersen and Luxton, 1982). Patchy distribution of either food or soil water is the most likely cause of non-random dispersion and aggregations of the mesofauna (Usher, 1976). However, the factors causing clumped distributions of the meso- and macrofauna are manifold. Some arbitrarily selected examples are given in the following paragraphs.

Moisture. Many Cryptozoa (like Isopoda, Diplopoda, Chilopoda or slugs) escape the extremes of water stress by aggregating in moist places and restricting their foraging to the night (Wallwork, 1976).

Chemical conditions. The pH may be important. The majority of earthworm species prefer soils with higher pH values (Piearce, 1972; Edwards and Lofty 1977) (see Chapter 14). The concentration of nitrogen may influence aggregation of the mesofauna (Usher, 1976; Wallwork, 1976). The pill millipede *Glomeris marginata* is frequently localized around nitrogen-rich sites, such as decaying logs containing large quantities of frass and faecal material produced by wood-boring insect larvae. In low-lime soils some slug species are responsive to calcium levels. Some species are more abundant under trees whose foliage has a high calcium content (Beyer and Saari, 1977). Secondary plant substances such as juglone under walnut trees may depress densities of soil arthropods (Summers and Lussenhop, 1976).

Herb layer. The type of ground vegetation can influence the distribution of dipterous larvae. For instance, many species in a German beech-wood on limestone preferred patches with *Lamiastrum galeobdolon*, ceratopogonid and some empidid larvae avoided areas with *Galium odoratum* (Hövemeyer, 1984). The woodmouse *Apodemus sylvaticus* was concentrated in vegetation providing ground cover if the competitor *Clethrionomys glareolus* was absent (Montgomery and Bell, 1981).

Canopy layer and tree trunks. The type of litter originating from different tree species can influence the distribution of at least the primary decomposers. However, the majority of litter animals (for instance, slugs, Beyer and Saari, 1977) do not form specific associations with trees. How are the soil and litter animals related to the distribution of tree trunks which are characterized by a specific microenvironment? A narrow region near the base of the stem, usually at one side, receives more than 10% of the rain via stem-flow (Ulrich et al., 1981). Slugs and snails (for instance, many Clausiliidae: Corsmann, 1981 and pers. comm., 1986) feeding on the algal mats on the bark of the trees concentrate near the base of the stems. Concentration near and feeding on tree trunks was observed for some Collembolar, too (Wolters, 1983). In July the density of the Collembola in a mull beech forest was 1.55 higher near the base of beech stems than in plots further away (Wolters, 1985). Some springtails, such as *Tomocerus flavescens, Allacma fusca, Orchesella flavescens, T. vulgaris*, climb onto the trunks of trees during humid weather and feed on algae and lichens (Bowden et al., 1976; Bauer, 1979; Wolters, 1983, 1985). Streit (1982) observed larger-scale aggregations of springtails and mites around trunks of beech (*Fagus sylvatica*) trees often measuring several metres in diameter.

Microhabitats like tree stumps (see below), logs, macrofungi or carrion are sites of a special fauna. The structure of litter is an important determinant of distribution and abundance (see below).

Most often a *complex of factors* governs the local distribution of animal populations. For example, soil depth, soil moisture characteristics, standing crop of litter and ground vegetation type all influenced the distribution of earthworms in an English beech woodland (Phillipson et al., 1976). Indirect effects of a variable may be important. For example, high levels of calcium increase the pH of the soil, which increases the activity of nitrifying bacteria, and alters the degree of organic matter incorporation and the C:N ratio (Beyer and Saari, 1977). Interactions such as these make the analysis of cause and effect in the distribution pattern of forest animals extremely difficult (Usher, 1976). Relevant scale is also a major consideration. According to Anderson (1977), large animals are distributed in relation to macro-environmental parameters (pH, rainfall, soil organic-matter content, base saturation, etc.), which can easily be measured on a scale relevant to the organism. The majority of the soil and litter fauna, however, are distributed in a mosaic of microsites, which is difficult to sample on a scale small enough to elucidate the effects of different factors on distribution.

Aggregation and patchiness surely have an important biological meaning: enhanced survival in favourable microsites, exploitation of appropriate food resources, maintenance of high population density in a small area (Usher, 1976), enhancement of reproduction efficiency, activity in a zone of preferred abiotic conditions, amelioration of the environment.

Structure and quality of the litter. Variables of litter structure are: litter depth, microclimate, number and size of air spaces, spatial arrangement and architectural properties (shape) of litter units (leaves, twigs, etc.). In addition, litter quality can affect the distribution of litter-inhabiting populations. In a broadleaved forest in the Karpaty foothills diplopods preferred areas with a high proportion of hornbeam (*Carpinus betulus*) litter, attaining densities up to 87 m^{-2}; in pure beech — an unfavourable food resource — density values were as low as 30 m^{-2} (Striganova, 1974). In a beech forest, litter of the herb *Allium ursinum* had a negative effect on the density of the collembolan species *Hypogastrura denticulata* and *Folsomia quadrioculata* and a positive effect on *Onychiurus scotarius* (Wolters, 1985).

There are some studies on the relation of spider populations to litter structure. Population density and diversity of litter spiders of different habitats appears to be positively correlated with litter abundance and depth (Uetz, 1979). Experiments with artificial leaf litter were performed by Bultman and Uetz (1982) which separated effects of litter as a nutritional base for prey, and as a spatially heterogeneous physical environment on litter-dwelling spiders. Litter nutrient content and structural complexity (form of artificial leaves) only slightly affected the species composition and richness of the spider population. In contrast, litter depth was the most influential component. Stevenson and Dindal (1982) demonstrated that the richness and density of spider species were significantly greater in curled than in flat leaves.

This was true for hunting as well as web-building spiders. In a beech forest, the abundance of the funnel-web spiders *Coelotes terrestris* and *Histopona torpida* was raised significantly by offering plastic tubes mixed with deciduous litter (Stippich, 1986).

Microhabitats on the ground. As already mentioned different microhabitats ("general system" of Elton, 1966) contribute to the complexity of the climax woodland floor (Wallwork, 1976). One can recognize the following major types: decaying wood and stumps, macrofungi, dead animals (vertebrates and invertebrates), dung, burrows of mammals, grass tussocks, stones on the forest floor, earthworm burrows and worm casts. The latter microstructures were preferred by Collembola (Loksa, 1978) and oribatid mites (mainly *Oppia*: Bayoumi, 1978) in a Hungarian hornbeam–oak forest. This preference appears to have a nutritional basis, especially in autumn. The total organic matter content, the C:N ratio and the percentage of tannins and lipids indicated that the chemical breakdown of the leaves in the burrows of the large-bodied earthworms was more advanced than in the surrounding areas (Szlavecz, 1985). In late spring and early summer the litter was chemically more homogeneous. Presumably the habitat preference at this time of the year can be explained by the higher moisture content of the burrows.

Quantitatively important in deciduous forest ecosystems are fungal sporophores, decaying wood and stumps. Many authors have studied the invertebrate fauna of macrofungi (cf. Elton, 1966; Wallwork, 1976; Martin, 1979), which are preferred by certain Diptera, beetles and slugs. Beyer and Saari (1977) demonstrated that the distribution pattern of the slug *Arion subfuscus* was related to the occurrence of macrofungi. There are numerous studies on the animal component of dead wood (cf. Elton, 1966; Fager, 1968; Wallwork, 1976). A very thorough investigation was performed by Derksen (1941) on pterygote insects. In a beech-wood on limestone the stump fauna and the fauna of the adjacent litter areas were sampled with photo-eclectors (emergence traps; see Southwood, 1978a). Many arthropod species (microphytophages such as Diptera and some staphylinid beetles, predators such as spiders and staphylinids) were typical inhabitants of the tree stump (Table 6.2). Some physical and biological properties of the soil beneath decaying wood may be modified significantly. Ausmus (1977) reported that organic matter in soil under logs in a deciduous forest increased four-fold, adenosine triphosphate (a measure of microbial biomass) eight-fold, root biomass more than two-fold, and calcium concentration five-fold.

Case study: aggregation in forest Collembola. Wolters (1983) analysed the distribution of Collembola in the soil and litter of a beech-wood on limestone near Göttingen in West Germany (see Chapter 14) using the Morisita index (Morisita, 1962). *Folsomia quadrioculata*, *Hypogastrura denticulata*, *Isotoma notabilis*, *Isotomiella minor*, *Megalothorax minimus*, *Tomocerus flavescens*, and *Tullbergia krausbaueri* had a non-random, aggregated distribution. Goodness-of-fit tests showed that the negative binomial distribution described the spatial pattern of those species which had been sufficiently sampled. For many species the type of distribution changed through the year. During the spring reproductive period more populations were clumped than during summer. In some populations (for instance, *H. denticulata*, *T. flavescens*) the degree of clumping decreased with increasing density. Only in *F. quadrioculata* were density and the tendency to occur in clumps positively correlated. Some species were restricted to microhabitats like moss (*Isotoma violacea*) or dead wood (*Hypogastrura burkilli*, *Tomocerus minor*). *Tullbergia callipygos* preferred areas where the forest floor was covered with *Anemone nemorosa*, possibly due to the lower pH values of these patches. In field experiments Collembola were attracted by certain species of soil fungi, especially by *Trichocladium opacum* (Wolters, 1985).

A key factor governing the distribution of Collembola is moisture, of both the soil and litter layer (Joosse, 1981). Many Collembola require high humidity because they have low resistance to water loss. They are only imperfectly capable of regulating their cuticular transpiration, but some species can absorb water vapour (Mais, 1970). Even species with high resistance lose the ability to regulate transpiration during their frequent moultings (Joosse, 1971). The relation of Collembola to soil moisture leads to temporal changes in spatial

TABLE 6.2

Some arthropod groups sampled with a stump photo-eclector and ground photo-eclectors (emergence traps, each covering 1 m^2) in a beech-wood on limestone (Göttinger Wald) during 1980

Species or families	Stump eclector		Ground eclector	
	number of species	individuals (m^{-2} yr^{-1})	number of species	individuals (m^{-2} yr^{-1})
Araneida (adults)[a]	14	46	53	88.3
Amaurobius claustrarius		4		2.2
Tegenaria sylvestris		2		0
Meta mengei		4		1.2
Lepthyphantes pallidus		4		0.6
Lepthyphantes zimmermanni		18		5.6
Opilionida (juveniles and adults)[b]	3	30	8	21.7
Coleoptera: Staphylinidae (adults)[c]	24	115	45	65.6
Baptolinus affinis		12		0.1
Habrocerus capillariformis		13		0.8
Atheta sodalis		19		0.3
Aleochara sparsa		6		0
Other Coleoptera (adults)	40	135	71	36.1
Biploporus bicolor		5		0.1
Athous subfuscus		13		6.4
Diptera (adults)[d]	31[e]	3864	35[e]	1721
Psychodidae		363		4
Chironomidae		86		127
Cecidomyiidae		347		661
Sciaridae		1077		303
Empididae		253		31
Phoridae		719		170
Sphaeroceridae		288		11

The 12 ground photo-eclectors were moved to new places every 4 weeks. Only important taxa are considered.
[a]Spiders: G. Stippich (pers. comm., 1981).
[b]Harvestmen and beetles: Schaefer (1986).
[c]Staphylinid beetles: Schaefer (1983a).
[d]Diptera: Hövemeyer (1984 and pers. comm., 1986).
[e]Families.

distribution. During dry weather, or during moulting or reproduction, most populations retreat to moist places (Verhoef and Nagelkerke, 1977). In some species, aggregation sites within the litter layer are marked by short-distance pheromones; obviously the aggregation pheromones are not strictly species-specific, but seem to attract other collembolan species, too (Verhoef et al., 1977). These aggregations in Collembola contribute to high population densities (Usher, 1976), to the enhancement of reproductive success (Joosse, 1970; Verhoef et al., 1977), and to the promotion of microbial processes by activation of the enzyme–substrate complex (Von Törne, 1974) and thus better exploitation of food.

The dependance of collembolan aggregations on environmental factors may be complex. This is exemplified by the different ecological behaviour and adaptation of the species pair *Orchesella cincta* and *Tomocerus minor*. Population patches of *T. minor* in a Dutch pine forest were totally restricted to water-saturated places. *O. cincta* assembled in very moist places during ecdysis and reproduction, a behaviour which led to dense aggregations; during the subsequent feeding period, however, the animals dispersed. Food shortage, presence of other species or high numbers of conspecifics may enhance this effect. After feeding, orientation to water-saturated places occurred by orthokinetic reactions, and the aggregations were re-established (Verhoef and Nagelkerke, 1977). In a habitat where moisture is heterogene-

ously distributed and wet and dry seasons alternate, and where *O. cincta* and *T. minor* coexist, the first species dominates due to physiological resistance to desiccation, high mobility between dry and wet areas, ability to escape predators and flexible reproduction (Joosse, 1981).

Vertical distribution

Stratification of the macro- and mesofauna in a beech forest. In a mull beech forest on limestone, most animal taxa of soil and litter occur in the organic strata L and O_f[1] and/or the upper soil layers (epedaphon and hemiedaphon[2]) (Fig. 6.1). Only some groups penetrate deeper into the soil (euedaphon[2]) — the Lumbricidae, Nematoda and other semiaquatic groups, Protura, larvae of Diptera and to a lesser extent the mesoarthropods Collembola and Acarina. The macroarthropods are rather strictly confined to the litter layer and to soil depths above −3 cm.

Generally most soil fauna populations are concentrated within the upper 5 to 10 cm of the soil (Petersen and Luxton, 1982). The soil fauna of forests with a thick, loose organic topsoil (mor type) may be distributed evenly through the full depth of this organic layer, and thereby reach a more extended vertical distribution than is usual in forests (see Chapter 14).

Relation to environmental gradients. In the forest soil there are gradients in physical factors, quality and abundance of food resources, and biotic interactions like predation pressure or competition. The surface subhorizons are usually characterized by low microhabitat complexity, and by unstable microclimates (Anderson, 1977).

A traditional line of study is the examination of the adaptions and tolerances of soil organisms to the extreme environmental conditions of the lower horizons of the soil–litter subsystems (see Wallwork, 1976). Oxygen concentration usually decreases and carbon dioxide concentration increases with increasing soil depth. Air in the soil is

[1]For explanation of symbols used for litter and soil horizons, see p. 517.

[2]Euedaphon: organisms living in deeper soil layers (adj. euedaphic); hemiedaphon: organisms living in upper soil layers and litter (adj. hemiedaphic); epedaphon: organisms living on the soil surface, sometimes penetrating into the litter or upper soil (adj. epedaphic).

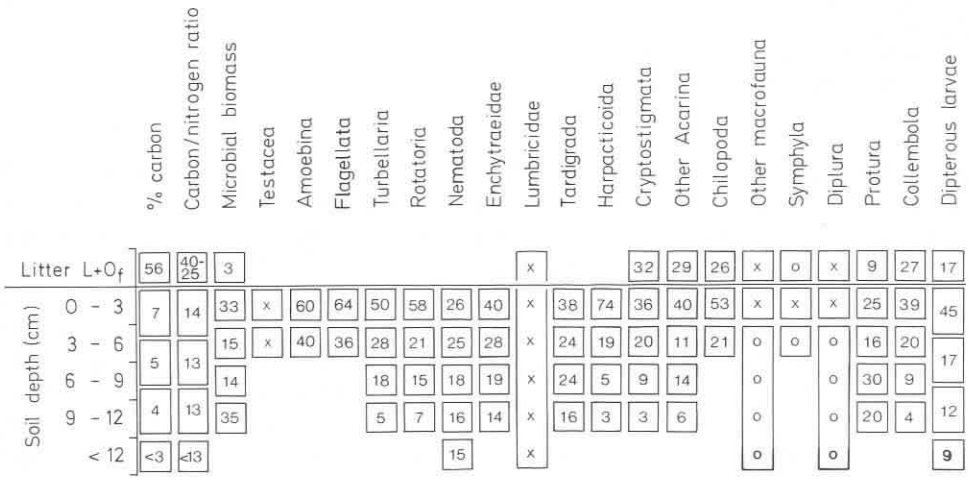


Fig. 6.1. Vertical distribution of the soil and litter biota in a beech forest on limestone with a mull soil (Göttinger Wald). The rectangles indicate the compartments analysed. Numbers are % of the total population. Most values refer to the annual mean of population density for 1980, 1981 or 1982; the microbial biomass refers to the 28th week of 1981. % carbon: % organic C of soil dry wt. ×: high value, ○: low value. Based on mostly unpublished data from R.G. Jörgensen (soil parameters), K.H. Domsch and M. Vanselow (microflora), R. Meisterfeld (Protozoa), A. Mellin (Enchytraeidae), U. Heitkamp (Nematoda), V. Büttner (other semiaquatic groups), H.-D. Baaske (Cryptostigmata, other Acarina), T. Poser (Chilopoda), Wolters (1983, 1985 and pers. comm., 1986) (Protura, Collembola) and Hövemeyer (1984, 1985 and pers. comm., 1986) (Diptera).

separated from the surface by water films and columns, leading to high concentrations of carbon dioxide which may be toxic for animals.

There is a correlation between the distribution of organic matter in the soil profile and the vertical distribution of invertebrates (cf. Fig. 6.1). However, it is uncertain if the distribution patterns of soil animals are determined by specific types of food (Anderson, 1977; Swift et al., 1979). This possible relationship is a much neglected field of study.

For some groups the ecological and physiological traits of the species have been correlated with soil depth. Life history characteristics and life forms depend on the preferred soil stratum. The Lumbricidae are a well-studied group. They belong to three principal life forms (Bouché, 1972, 1977; Perel', 1977; Satchell, 1980) all of which are represented in forest mull soils: (1) the surface-active, pigmented litter-dwellers (for instance, *Dendrobaena mammalis*, *D. octaedra*); (2) the organic-horizon dwellers, which construct branching horizontal burrows (such as *Aporrectodea rosea*); (3) the deep burrowing forms, which come to the surface at night and draw litter down (such as *Lumbricus terrestris*). These three types are termed "epigées", "endogées" and "anéciques" according to Bouché (1972, 1977), who gave a detailed account of the adaptations of species belonging to these different life forms. As an example the mesofauna (mainly Collembola and Cryptostigmata) is analysed in more detail in the following paragraph.

Case study: Mesofauna. Studies in some forests have related typical ecological characters of the mesofauna to increasing environmental stability with depth.

Petersen (1980) gave a thorough analysis of the springtail fauna (Collembola) in a Danish beech forest. Some life-form characteristics are listed in Fig. 6.2. The small individual size and the short appendages of euedaphic species are an adaptation to the narrow space of interstices. Surface-living species move a lot and tend to have higher respiratory rates than deeper-living species, provided specimens of similar weight are compared (Petersen, 1981). Collembola living superficially have, according to Bödvarsson (1970), a higher percentage of fungal hyphae and spores in their gut than species living deeper in the soil, and Wolters (1985) found fewer mineral particles. Euedaphic species are obliged to feed more or less continuously on poor food, the epedaphic species must spend much time and energy in search for better quality food (Petersen, 1980). In the complex system of soil interstices, indirect sperm transfer is too inefficient, therefore parthenogenetic populations are favoured (which are not threatened by unstable environments as in the surface layer). The low number of eggs per oviposition (as a consequence of small body size) is compensated for by an extended period of reproduction with repeated oviposition, which is rendered possible by the constant environmental conditions in the deeper layer of soil. The nutritional aspect of the "life-form theory" proposed by Petersen (1980) is questioned by Wolters (1985), who found no difference in the amount (measured as energy content) of spores, fungal hyphae and amorphous organic material in the guts of epedaphic and euedaphic Collembola of a mull beech forest, the only exception being algae and pollen utilized by surface-living, not by soil-living species.

Are the biological traits within the springtails paralled in the other important mesofauna group, the oribatid mites (Cryptostigmata)? Litter mites are partly large-bodied, although several exceptions occur (such as *Oppiella nova*). It is difficult to generalize about the forms found in wood or the upper litter layer (Abbott et al., 1980). The forms of the lower litter and soil are mostly smaller, lighter-bodied mites. However, large mites can penetrate deep into the soil by following channels produced by rotting roots, while smaller mites may be attracted to refugia by woody litter. Small oribatid mites tend to be detritus-feeders (Anderson 1971, 1975b). Luxton (1981b) found that the litter-dwellers among the moss mites of a Danish beech forest carry the greater numbers of eggs; the females of most of these species bear eggs at all time of the year. Parthenogenetic mites live mostly below the litter layer.

Obviously Collembola and oribatid mites show similar patterns in adaptation to vertical gradients in the soil. However, further studies about microarthropod life forms are necessary since extensive descriptive analyses are few and experimental evidence is still incomplete.

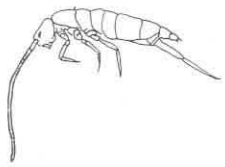
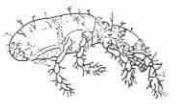
	Epedaphon	Euedaphon
Collembola		
Cryptostigmata		
Vertical distribution	Surface, litter	Soil interstices
Body size	Large	Small
Appendages	Long	Short
Colour	Pigmented	Not pigmented
Food	More fungi (high quality)	More detritus (low quality)
Metabolic activity	High	Low
Life cycle and reproduction	Bisexual, seasonally defined, many eggs, small progeny	Parthenogenetic, throughout the year, few eggs, large progeny

Fig. 6.2. Life forms of forest Collembola and oribatid mites (Cryptostigmata) in relation to vertical distribution. Data for Collembola mainly from Petersen (1980), for Oribatei from various authors (see text).

Seasonal vertical migrations. Animals in temperate deciduous forests may migrate vertically as an adaptation to seasonal changes in temperature, moisture or other factors. Medium-sized animals display the most pronounced vertical movements. The microfauna does not move over large distances, and many larger litter-dwelling animals cannot penetrate into the soil. The fauna of a German beech-wood on limestone may serve as an example (Fig. 6.3). The earthworms concentrate in the B horizon in winter, except for adults of the deep-burrowing species *Lumbricus terrestris*, which remain in the C horizon. The Chilopoda, representatives of the macrofauna, penetrate deeper into the soil during that time of the year, as do springtails. However, dipterous larvae are active in the litter layer and the topsoil even during winter.

Macroinvertebrates. The majority occupy the litter in the summer and occur in or near the soil layer in the winter months. Most members of the macrofauna in the above-mentioned beech forest change preferred strata seasonally. In winter, species concentrate between the litter layer and the soil, and in the topsoil layer. Digging and some non-digging animal populations (such as clausiliid snails) migrate further downwards, using partly preformed burrows and holes — for instance, near the roots of plants.

A typical forest species such as the isopod *Trichoniscus pusillus* migrates from the litter to the soil at the onset of winter (Standen, 1973). The vertical distribution of the millipede *Glomeris marginata* changes markedly around 6°C (Bocock and Heath, 1967). Individuals will migrate from

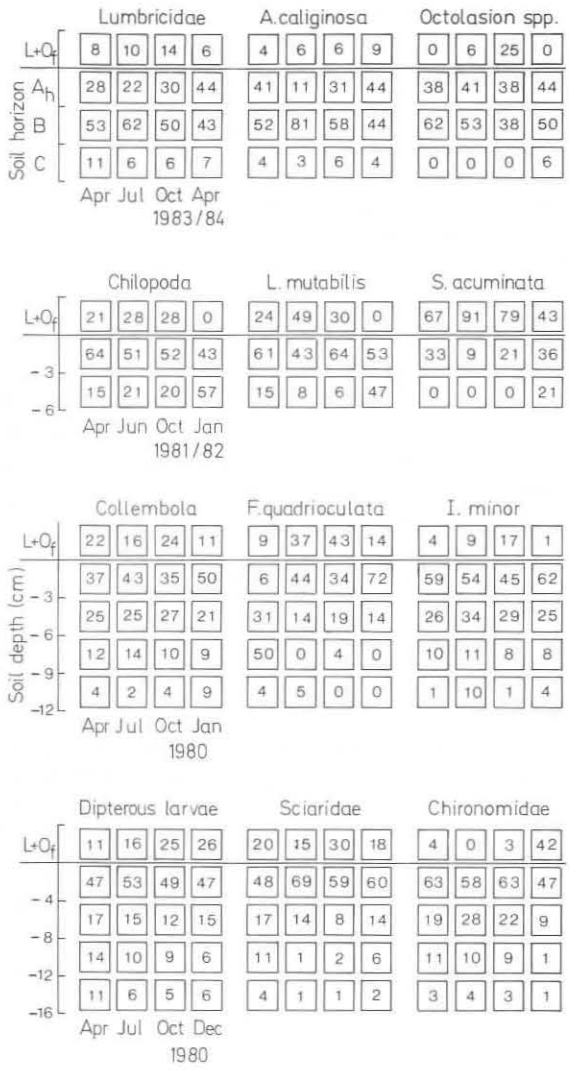


Fig. 6.3. Vertical distribution of some soil and litter animal groups in a beech-wood on limestone with mull soil (Göttinger Wald) at four times of the year. The rectangles indicate the compartments analysed. On the left side total population of Lumbricidae, Collembola, Chilopoda and dipterous larvae, in the middle and on the right side 2 species (2 families for the Diptera) as an example L. mutabilis = *Lithobius mutabilis*; S. acuminata = *Strigamia acuminata*; F. quadrioculata = *Folsomia quadrioculata*; I. minor = *Isotomiella minor*. Numbers are % of the total population. Based on mostly unpublished data from M. Judas (Lumbricidae), T. Poser (Chilopoda), Wolters (1983 and pers. comm., 1986) (Collembola) and Hövemeyer (1984 and pers. comm., 1986) (Dipterous larvae).

the litter and surface soil and reduce feeding when the mean daily temperature falls to *c.* +6°C. The millipede *Blaniulus guttulatus* was observed by Brookes and Willoughby (1978) at a soil depth below 20 cm in a British oak woodland during summer, autumn and winter. The decreasing numbers in the surface layers are explained by the fact that the animals are moulting, building nests and laying eggs at these times. Together with adults, large numbers of younger stadia appear in the surface layers in spring.

Changing temperature is thought to be the main stimulus for the vertical migration of soil macroinvertebrates, but other factors such as humidity of air and dryness of the soil and the availability of food resources may be important. However, the importance of seasonal vertical migrations for the forest macroinvertebrate fauna is generally overestimated.

Mesofauna. In a North American cove hardwood forest Collembola (Onychiuridae and Entomobryidae) and Oribatei increased migration to the litter layer with rising temperature in spring (McBrayer et al., 1977). In a German beech forest Collembola (Wolters, 1983, 1985) and Oribatei (H.-D. Baaske, pers. comm., 1986) shifted their population maximum to deeper strata of the litter–soil subsystem during winter and summer (cf. Fig. 6.3). In a Danish beech forest the adults of several oribatid species rose to the litter layer during spring (Luxton, 1981c). However, Anderson (1971) found a relatively stable population of oribatid mites in the O_f and O_h layer of a *Castanea* and a *Fagus* woodland during the whole year.

Generally temperature is assumed to induce vertical migrations of soil mesofauna populations. However, Wolters (1983) observed a close correlation between vertical distribution and temperature only for one species of the collembolan fauna, *Folsomia quadrioculata*. According to McBrayer et al. (1977), the cue for vertical migrations seems to be changes in the moisture gradient. However, Vannier (1970) presented evidence that normal variations in forest soil moisture do not affect microarthropod vertical distributions. Luxton (1981c) assumed that oribatid mites use the spring flush of microfungal growth or pollen input, and emphasized that generalizations about vertical migrations and their causes are not currently substantiated. He attributed seasonal migrations of oribatid mites to two main reasons: (1) escape from adverse environmental conditions in the surface layers as the result of extreme changes in temperature and/or moisture, and (2) exploitation

of seasonally available food and/or space resources. Gist and Crossley (1975) created a very speculative hypothesis to explain the seasonal pattern of vertical movement in the soil and litter layer. During summer, microarthropods avoid contact with the larger litter macrofauna by remaining in the soil for most of the time. As the litter temperature decreases the activities of the larger litter invertebrates slow down, ceasing in late autumn. After litter fall, microflora biomass rises and is used by the mesofauna as a food resource. The small invertebrates reproduce, and their progeny remain in the litter until the larger invertebrates become active again.

In summary, there are many problems in analysing vertical migrations of litter and soil animals; they concern clear-cut evidence of population movements as well as the evaluation of the underlying proximate and ultimate factors.

Diurnal migrations. Not much is known about diurnal vertical movements of soil and litter fauna. Surface-feeding earthworms migrate to the litter layer during night. Moisture-requiring slugs and night-active predators leave their shelters during the dark time of the day. By using the ^{137}Cs method, McBrayer and Reichle (1971) observed that soil-dwelling mycetophagous and saprophagous populations of Collembola and Oribatei feed primarily at the soil surface. These authors even suggested that feeding by predators also might occur at the soil–litter interface.

Rhizosphere and mycorrhizae

Microbial activity is generally increased around roots. This enhancement results not only from symbiosis between mycorrhizae (see Chapter 9) and trees, but also from organic root exudates, decaying root material, differences in oxygen and carbon dioxide concentrations, and high concentrations of water and mineral nutrients (Rovira, 1965).

The "mucigel" — a layer of mucilaginous material, through which water and ions can pass rather freely — normally covers the young root. The mucigel and the region close to the root (the rhizoplane) are richer in micro-organisms than the bulk soil (the rhizosphere). Root exudates contain organic acids, sugars and amino acids or amides. A major source is the zone of the root immediately behind the tip (Rovira and Davey, 1974). Pathogenic rhizosphere microbes can damage plants, but other micro-organisms are responsible for more subtle effects involving decomposition, ammonification, nitrification, denitrification or phosphate availability.

Some members of the soil animal community — root feeders (nematodes), feeders on fine roots (some oribatid mites), bacteriophagous and mycetophagous groups (such as rhizopods) — are concentrated in the rhizoplane and rhizosphere. Do activities of soil animals influence the rhizosphere? Do animals affect the distribution and abundance of mycorrhizae, so important to forest trees (Marx and Bryan, 1975; Ellenberg et al., 1986)? Soil arthropods apparently can influence, perhaps regulate, nutrient uptake by plants by consuming fine roots or by affecting the rhizosphere microflora (Crossley, 1977) (see Chapter 9). However, the extent and importance of such effects are unknown (Usher et al., 1982).

Maser et al. (1978) found that small mammals are primary agents of spore dissemination of hypogeous mycorrhizal fungi, particularly higher Basidiomycetes, Ascomycetes, and Phycomycetes (Endogonaceae). The spores pass through the digestive tract and are excreted without loss of viability. Fungus consumers in a coniferous forest and other habitats in Oregon were gophers (Geomyidae), jumping mice (Zapodidae), mice (Cricetidae), pikas (Ochotomidae), rabbits (Leporidae), shrews (Soricidae), squirrels (Sciuridae), and voles (Microtidae).

Influence of animals on forest soil and litter

Animals directly affect the soil and litter subsystem in numerous ways. The impact of the fauna may be through transformation or translocation of material. Transformation is mainly a component of decomposition (Swift et al., 1979; see Chapter 9), but may also lead to the formation of humic substances and the modification of the soil crumb structure. Translocation, which is not yet adequately investigated, is especially important in mull soils (see Chapter 14).

Turnover of the soil by lumbricids is important in many forests. *Octolasion lacteum* had a soil intake of 4.0 mg h^{-1} in a *Liriodendron* forest, as measured in the laboratory by tagging soil with radioactive caesium (^{137}Cs) (Crossley et al., 1971)

— that is, an intake of 28.8% of the live weight per day. According to Bolton and Phillipson (1976), *Aporrectodea rosea* consumed 133 to 516 mg per gramme fresh weight of worm per day beneath bramble in a mixed deciduous forest. Scheu (1987) calculated that annual faeces production by endogeous earthworms in a German beech forest corresponded to a soil layer of 9 mm. As a result of the feeding and burrowing activities of the earthworms the mineral and organic components of the soil become thoroughly intermixed, and the formation of organomineral complexes, which are such a characteristic feature of fertile soils, is promoted. Zlotin and Khodashova (1980) emphasized the importance of the burrowing activity of vertebrates in a forest–steppe ecosystem. Thus both earthworms and small mammals translocate soil material; macroarthropods are less important in this system.

Different authors (for instance, Babel 1975; Webb, 1977) have documented the dominance of invertebrate faeces ("dropping fabrics") in the micromorphology of forest soils. Some of the faeces particles are very resistant to environmental degradation. Schuster (1956) observed that oribatids did not consume faeces of isopods and iulids. Zachariae (1965) describes the manifold activities of animals during the process of decomposition and the formation of soil structure in central European beech forests, leading to "animal traces" in the soil profile: destruction and comminution of litter, excrements and droppings of different kind, passages and pits in the soil (produced mainly by earthworms), loosening and blending of the earth.

The vegetation subsystem

The vegetation subsystem is characterized by a strong seasonality in structure. Special microhabitats that occur in the canopy layer, such as tree holes (Kitching, 1971) or sap flow (Elton, 1966), are not dealt with in this context here.

Vertical distribution

According to Elton's (1966) system three layers within the vegetation subsystem can be distinguished: the herb, the shrub and the canopy layers. Tree trunks appear to be a fourth zone.

To what extent is the herb layer, which is in some forests with mor soils almost totally lacking, a stratum independent of the ground zone? The herb layer is interwoven with the litter layer during the season of activity of the macrofauna, such as slugs, snails, predatory arthropods. However, some species, especially phytophagous insects, are more or less bound to the herb layer. An example is the flea beetle *Hermaeophaga mercurialis* feeding on *Mercurialis perennis*. But even predatory forms, like some staphylinid beetles (Schaefer, 1983a) — for instance *Eusphalerum* spp. — are confined to the herb layer during their period of activity.

Only a short analysis of the fauna of the trunks and of the foliage in the canopy and shrub layer is given in the following paragraphs.

Trunks of trees and shrubs. The fauna of tree trunks comprises a heterogeneous group of migrants and permanent residents, mainly microphyte feeders and predators. Spiders, Collembola, Psocoptera, beetles and Diptera dominated among the arthropods found on trunks in a German beech forest on limestone (Table 6.3). Funke and Sammer (1980) found the dominant animals on tree trunks of a beech forest in southern Germany to be Collembola, Diptera (mainly saprophagous); among predatory arthropods Araneida, Opilionida, Staphylinidae (dominant *Leptusa ruficollis*); among the phytophagous groups Lepidoptera, Rhynchota and Thysanoptera; and parasitic Hymenoptera. Microclimate, microstructure and occurrence of epiphytes are important environmental factors for the bark animal community. Only few species dominate on smooth bark (for instance of beech trees, *Fagus sylvatica*), whereas a highly diverse fauna lives on fissured bark (for instance of oak trees, *Quercus robur*) (Nicolai, 1986).

The composition of the animal community on tree trunks depends very much on weather conditions. During wet humid weather, which favours the growth of epiphytic algae and positive water balance, many animal populations migrate onto the bark from the litter and soil layer, including Gastropoda (slugs, Clausiliidae) (M. Corsmann, pers. comm., 1986) and Collembola (Bowden et al., 1976; Bauer, 1979; Wolters, 1983, 1985). The Collembola are active mainly during the night and on the lower parts of the tree trunks near the ground (Bowden et al., 1976). Fog (1979b) emphasized that the activity of animals on the stumps of beech trees is mainly determined by the availability

TABLE 6.3

Arthropod groups sampled with an arboreal photo-eclector and with ground photo-eclectors in a beech-wood on limestone (Göttinger Wald) during 1980

Species, families or orders	Arboreal eclector		Ground eclectors		Number of species in both eclector types
	number of species	adult individuals yr^{-1}	number of species	adult individuals ($12\ m^{-2}\ yr^{-1}$)	
Araneida[a]	40	382	52	1047	24
Amaurobius fenestralis		53		4	
Coelotes terrestris		14		81	
Theridion pallens		12		3	
Drapetisca socialis		72		6	
Linyphia triangularis		87		92	
Gonatium rubellum		33		38	
Walkenaera cuspidata		29		116	
Opilionida[b,c]	3	+	7	+	3
Collembola[c,d]	≥15	+	25[f]	++[f]	
Orchesella flavescens		+		+	
Entomobrya corticalis		+		+	
Tomocerus flavescens		+		+	
Psocoptera[b]		+		(○)	
Thysanoptera[b]		+		+++	
Heteroptera[b]	13	666	12	49	5
Anthocoris confusus		173		13	
Blepharidopterus angulatus		34			
Miris striatus		147		3	
Phytocoris tiliae		158		1	
Auchenorrhyncha[b]	9	3822	14	835	5
Eupteryx stachydearum				224	
Fagocyba cruenta		3803		517	
Speudotettix subfusculus		1		58	
Coleoptera[b]					
Staphylinidae	7	316	45	787	7
Anthophagus angusticollis		163		58	
Leptusa fumida		31		4	
Leptusa ruficollis		112		5	
Elateridae	4	154	4	125	3
Athous vittatus		92		43	
Athous subfuscus		60		77	
Scolytidae	1	330	2	11	1
Xyloterus domesticus		330		8	
Hymenoptera[c]		+		+	
Diptera[e]	26[g]	1693	34	1771[h]	
Tipulidae		174		1.5	
Cecidomyiidae		1056		661	
Rhagionidae		6		1.8	
Empididae		11		31.3	
Phoridae		132		169.7	

The arboreal photo-eclector encircled the beech tree in a height of 4 m above the ground. The 12 ground photo-eclectors covered an area of 1 m^2 each and were moved to new plots every 4 weeks.

[a]Data from G. Stippich (pers. comm., 1986).

[b]Data from Schaefer (1983 and unpublished results).

[c]○, +, ++, +++ = present in very low (○), low (+), high (++), very high (+++) numbers.

[d]Data from Wolters (1983 and pers. comm., 1986).

[e]Data from Hövemeyer (1984 and pers. comm., 1986).

[f]Data from soil samples.

[g]Families.

[h]ind m^{-2} emerging per year.

of food resources, not by drought. Not much is known about diurnal activity rhythms of the trunk-inhabiting fauna, and differences between the populations on lower and higher parts of trunks.

Shrub and canopy layer. The different guilds in these two layers are free-living phytophages (such as Coleoptera, Hymenoptera, Lepidoptera), zoophages (such as Araneida, Hymenoptera), leaf miners and wood-boring insects. Important zoophages are ants (such as *Formica rufa*: Skinner, 1980). Temperate deciduous forests, particularly in North America, have an unusually rich and varied bird fauna which can exploit both canopy and floor food resources (insects, seeds, fruits).

For most arthropods the canopy provides a habitat for only part of the life cycle (Fig. 6.4). For example, the larvae of most Lepidoptera feed in the canopy, but drop to the ground to pupate. By contrast, many adult beetles, for example some weevils of the genera *Phyllobius* or *Polydrusus*, consume leaf material in the canopy, but during their larval phase are subterranean root feeders. However, some species do pass their complete life cycles in the canopy. Many of these arthropods are parasites of predators of plant feeders (for instance, species of the sheet web spider *Linyphia*), but most are phytophagous, using the tree not only as a structural element of their habitat, but also as food. Most of the tree-living leafhoppers (Typhlocybinae) have such life cycles (Claridge and Wilson, 1976). Some gall-inducing arthropods and leaf miners do not migrate to the ground (Segebade and Schaefer, 1979), while others (such as the weevil *Rhynchaenus fagi*) hibernate in sheltered places in the litter layer.

A dispersal phase is an obvious prerequisite to maintain populations of some species in the canopy layer. Connor et al. (1983) demonstrated that most populations of leaf-mining insects on oak (*Quercus*) trees are maintained by yearly re-

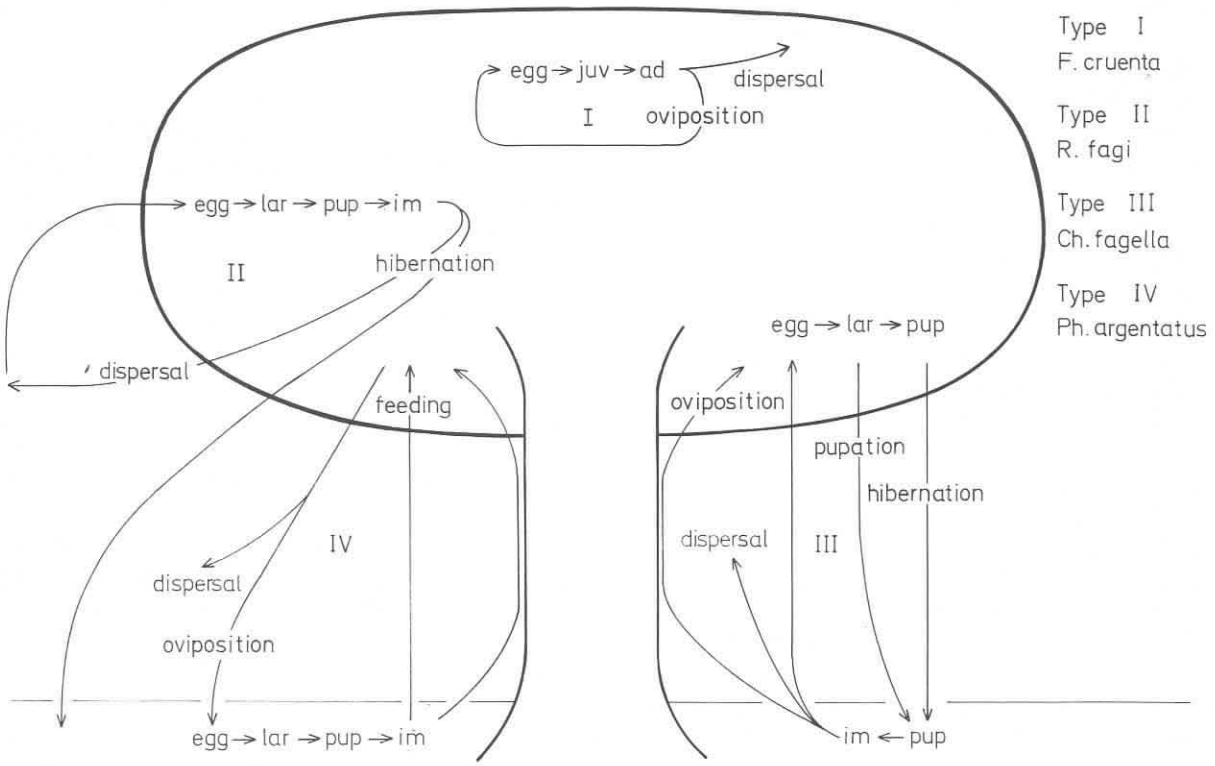


Fig. 6.4. Life-cycle pattern and migration of four phyllophagous insect species: *Fagocyba cruenta* (Typhlocybidae), the coleopterans *Rhynchaenus fagi* and *Phyllobius argentatus* and the lepidopteran *Chimabacche fagella*. lar: larva, juv: juvenile, pup: pupa, ad: adult, im: imago. Data from Nielsen (1975), Ellenberg et al. (1986) and unpublished results.

immigration from safe overwintering sites, and not from *in situ* reproductive recruitment.

Litter–vegetation interface. The microclimate between the litter layer and the strata above differs markedly in humidity, constituting a sharp boundary for many forest invertebrates. Only after longer periods of rain does the relative humidity reach values above 90% in a beech-wood (Bauer, 1979). Then drought susceptible animals appear in the vegetation layers, such as slugs or Collembola (see above). Climbing by Collembola is directly related to rainfall. No satisfactory explanation can be advanced for this activity, which takes place often and on a large scale. Increase of carbon dioxide concentrations in the leaf litter, or compaction following rain, may cause emigration from the leaf litter layer, but do not explain climbing (Bowden et al., 1976).

The interface is important in another respect: animals migrating upward from the soil to the vegetation layers have to pass a finely woven web of enemies such as spiders, opilionids, beetles, centipedes, pseudoscorpions and predatory Diptera larvae. In a German beech forest on moder soil, about 70% of the curculionid species *Phyllobius argentatus* and *Polydrusus undatus* migrating to the crown after pupation were killed by predators (Ellenberg et al., 1986).

Horizontal distribution

Animals that inhabit the vegetation layers and that depend on the species composition and structure of the vegetation are very patchily distributed (Nielsen, 1974). An important question is which factor influences the distribution of animal populations in herb and canopy layers: the species of plants, or the structure of the vegetation. It is becoming more obvious that zoophages among the insects, spiders, birds and mammals are more highly correlated with vegetation architecture (see p. 95) than with particular plant species.

On the other hand it appears that phytophagous animal species are more liable to be related to the distribution of the host plant species. Claridge and Wilson (1978) have discussed the importance of feeding and oviposition behaviour in the distribution patterns of woodland leafhoppers. Many species show extreme host-plant specificity, but there is a need to differentiate between records of feeding, oviposition and chance settling. Claridge and Wilson (1976) sampled the mesophyll-feeding leafhoppers in three broadleaved woodlands in South Wales and observed a distribution within the canopy very distinctly dependent on plant species. Many of the 35 leafhopper species were primarily associated with one host tree species. Only one leafhopper species was found on all tree species sampled. Futuyma and Gould (1979) emphasized that insects respond to many factors that differentiate plant species. Few of the 18 species of common woody plants in a mature upland forest (New York State, U.S.A.) had a highly distinct, specialized fauna of phytophagous lepidopteran and tenthredinid larvae.

The vegetation layers of the wood edge are characterized by a high species diversity (Elton, 1966). However, the wood edge serves as a transition zone for some animal populations that show daily (such as roe deer, *Capreolus capreolus*) or seasonal (such as the weevil, *Rhynchaenus fagi*: Grimm, 1973) migration patterns. Most members of the animal community in larger deciduous forest areas spend their whole life cycle within this habitat.

Distribution on the individual tree

It is well known that canopy animal populations are not distributed homogeneously in the crown zone of an individual tree. The bulk of studies concern forest birds (see p. 105). Nielsen and Ejlersen (1977) studied the distribution of phyllophagous arthropods in the canopy of a Danish beech forest. The leaf-mining moths *Phyllonorycter maestingella* and *Stigmella hemargyrella*, and the adult weevils *Phyllobius argentatus* and *Rhynchaenus fagi* mainly attacked the understorey. The weevils fed especially in the low canopy in the central part of the stand. Mines of *R. fagi* chiefly occurred in the top of the overstorey canopy or at the fringe of the stand. The same type of distribution of the mines of *R. fagi* was observed by Grimm (1973) in a German beech-wood. In the same stand the females of the moth *Chimabacche fagella* deposited their eggs chiefly in the lower canopy, where the feeding larvae remained concentrated (Winter, 1971; Ellenberg et al., 1986). Funke (1973) and Nielsen and Ejlersen (1977) suggested that in some cases the shade leaves of the understorey canopy may cushion the effect of

herbivory in the sun leaves of the overstorey canopy (see p. 183). Maiorana (1981) postulates that plant individuals incur greater herbivore damage in shaded than in sunny areas. This effect may be caused by the more extreme environmental conditions in sunny microhabitats.

Phyllosphere and phloeosphere

Leaf surfaces in general (the **phyllosphere**) support a diverse assemblage of micro-organisms. Jensen (1971) found counts of bacteria on leaves of beech (*Fagus sylvatica*) ranging from 3300 cm^{-2} in early summer to 31 700 in late summer. Cox and Hall (1978) detected 16 fungal species actively growing on oak (*Quercus robur*) leaves. Total numbers of colonies increased towards the end of the season, when the leaves grow old. Petelle (1981) postulates a mutualistic relationship between phyllosphere micro-organisms and their host plant. At the very least, the microbial mat would serve as a physical barrier to invasion by plant pathogens. Phyllosphere bacteria include a higher percentage of antibiotic-producing forms than do litter or soil bacteria (Jensen, 1971). On the other hand, it is unresolved whether fungal leaf saprophytes are beneficial or detrimental to the plant. Trees produce antimicrobial substances (Blakeman and Atkinson, 1981). Gallic acid in dew collected from Norway maple (*Acer platanoides*) may, in part, be the cause of low populations of *Cladosporium herbarum* on these leaves compared with those of other plants (Dix, 1974).

There is no definite information on animal consumers (mites, Psocoptera?) in the phylloplane, and their possible function in this microsystem.

The **phloeosphere** consists of the bark of trees and a diverse array of microphytes, and in some cases thallophytes such as mosses or lichens. Oribatid mites, snails and slugs and Psocoptera are typical microphyte grazers (Wallwork, 1976; Fog, 1977; Gjelstrup, 1979). Pschorn-Walcher and Gunhold (1957) found nematodes, tardigrades, myriopods, pseudoscorpions, mites (gamasid, trombidiid and oribatid species), and Collembola in moss and lichens on trees of parks and woodlots. A modification of the phloeosphere microsystem is the outer region of attached dead wood. The oribatid mite *Liebstadia humerata* preferred the subcortical space of standing dead wood, with a maximum density of 50 individuals per cubic centimetre of bark tissue in a Danish oak forest (Christensen, 1980). *L. humerata* is relatively tolerant of low moisture content.

The phloeosphere micro-ecosystem is strongly dependent on humid or wet conditions, because it is connected with the plant only through the rather impenetrable outer surface of the bark. Growth of epiphytic pleurococcoid algae begins at 68% relative humidity of the air, reaches one half of maximal photosynthetic rate at 90% relative humidity, and maximal rate of photosynthesis at 97 to 98% relative humidity (Bertsch, 1966). On hardwood stumps green algae tended to occur in low density when there was a high density of fungi and bacteria, and vice versa (Fog, 1977).

Fog (1979a) studied the snails occurring on 30 hardwood stumps in a Danish deciduous wood. Seven species of snails, which fed by grazing the wood surface, occurred with densities up to more than 200 m^{-2}. The snails — mainly Clausiliidae — showed a clear inverse relationship with the amount of green algae and yeasts. Only weak positive correlations, or none, were found with the amount of fungal hyphae. However, r values between snails and bacteria were 0.7 after logarithmic transformation. Bacterial density on the stump sides explained a greater part of the variation in snail numbers than density on stump planes. A severe drought did not by itself decrease snail or slug numbers, but indirectly affected them, possibly through changes in the stump microflora (Fog, 1979b).

DIURNAL RHYTHMS, SEASONALITY AND LIFE CYCLES

The temporal organization is a constituent of ecosystem structure. It is difficult to evaluate how the dynamics of the system are influenced by diurnal and seasonal rhythms of the animal community.

Diurnal rhythms

There are some comprehensive investigations concerning the macrofauna in the litter layer of deciduous forests. In a German beech–oak forest the diurnal rhythms were different for the different groups of the macrofauna (Löser, 1980). Carabi-

dae were mainly night-active, Diplopoda and Isopoda strictly night-active, the majority of Araneida day-active, Staphylinidae mainly day-active and the Opilionida night-active. Maximum activity of the Carabidae occurred before midnight, of the Opilionida after midnight; there were no signs of interference competition. For litter-dwelling predatory beetles in an English mixed deciduous woodland, Dennison and Hodkinson (1983b) found a positive correlation between beetle size and level of nocturnal activity. There was a seasonal trend: during the warmer periods of the year, activity of the total beetle community was divided symmetrically between day and night, but during the colder periods, daytime activity was predominant.

Thiele (1977) postulated that the mainly nocturnal habit of forest Carabidae was connected with high moisture requirements. The activity of other mainly nocturnal animals (such as earthworms, slugs) on or near the surface of the litter layer is also related to high moisture of this stratum.

There is not much information on diurnal activity rhythms of the invertebrate fauna in the forest vegetation layers and in the soil. Soil animals appear to have less pronounced daily activity cycles than animals which live above the soil.

Seasonality

Winters are often cold in temperate deciduous forests, but the warm, wet summers with only rare periods of drought allow a long season of growth and activity. There are numerous studies of seasonal fluctuations of animal taxa in both soil and vegetation. Often the data are global and an interpretation is not feasible. Nematoda, for instance, have the highest densities in winter (Phillipson et al., 1977); population density changes are not directly related to temperature, to rainfall, or to biotic influences. Obviously, a multiplicity of factors interact to govern seasonal changes.

For the soil and litter fauna of a German beech forest on limestone, the seasonal development of some taxa is illustrated in Fig. 6.5. Two peaks of density occur during the year: one in spring and one in autumn. The depression during summer, mainly in July and August, can partly be explained by the period of summer drought in the soil. High abundance in the spring, summer and autumn are generally determined by reproduction during that period of activity. The Oligochaeta (having a refugium in the soil) have high population numbers even during summer. The density of the microfaunal and mesofaunal groups (such as Collembola; Wolters, 1985) is not correlated with the biomass of the microflora, which fluctuates widely during comparatively short time intervals.

Life cycles

Lumbricidae. The time of development of many lumbricid species is about one year. The life span of mature earthworms may range to several years, although it is probably no more than a few months in the field (Satchell, 1967; Edwards and Lofty, 1977).

According to Rundgren (1977), deep-burrowing species have two emergence periods in southern Sweden. Strategy 1 is the bimodal-emergence/deep burrowing strategy, associated with low production of cocoons. The distribution of emergence times to two more or less synchronized peaks seems to balance the low cocoon production by dividing the risks, and ensuring the greatest survival of the newly emerged juveniles during periods of adverse climatic conditions and/or scarcity of food. Surface-living species have a single and relatively prolonged emergence period, from summer throughout the autumn. This strategy 2 (unimodal-emergence/surface-living strategy) is combined with a high cocoon production and with a wide horizontal distribution of cocoons due to high mobility of the surface-living species. The high production and the scattered distribution of cocoons in a varying surface layer ("spreading of risk"; Den Boer, 1968) may offset the disadvantage of a single emergence period and a deposition of cocoons close to the surface, where the greatest climatic variation and the heaviest pressure from predators may occur.

Other soil and litter macrofauna. Many macrofauna species are perennial, and individuals can reach an age of several years — for instance snails (M. Corsmann, pers. comm., 1986), Chilopoda (Albert, 1980; T. Poser, pers. comm., 1986) and Diplopoda (T. Sprengel, pers. comm., 1986).

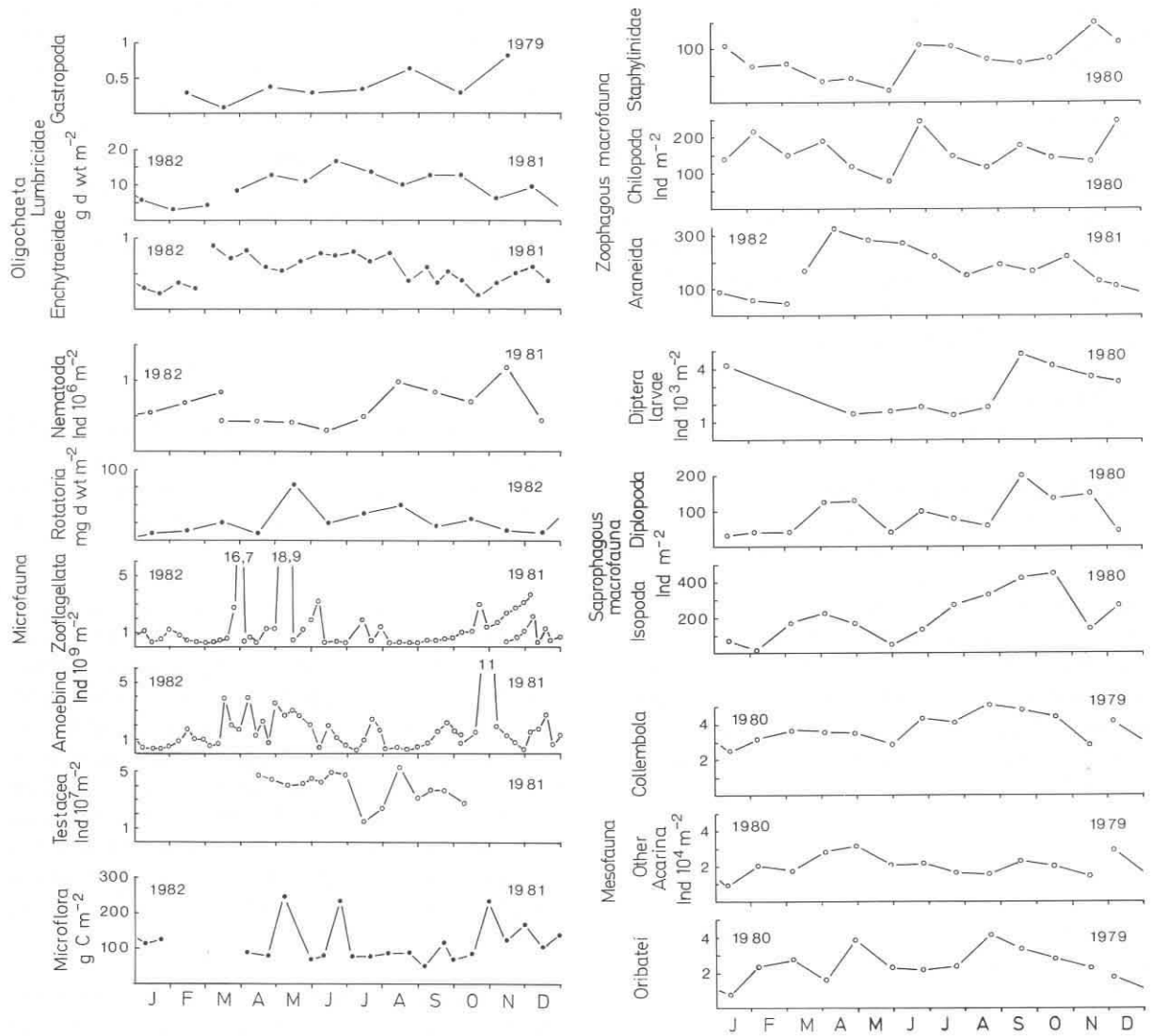


Fig. 6.5. Seasonality of soil and litter biota in a beech-wood on limestone (Göttinger Wald). Based on mostly unpublished data from K. H. Domsch and M. Vanselow (microflora), R. Meisterfeld (Protozoa), U. Heitkamp (Nematoda), A. Mellin (Enchytraeidae), V. Büttner (Rotatoria), M. Schaefer and H.G. Joger (Lumbricidae), Corsmann (1981) (Gastropoda), H.-D. Baaske (Acarina), Wolters (1983) (Collembola), T. Sprengel (Diplopoda), Hövemeyer (1984) (Diptera), T. Poser (Chilopoda), G. Stippich (Araneida), M. Schaefer (1983a) (Staphylinidae).

Soil and litter mesofauna. Many collembolan species are univoltine (Healey, 1971; Petersen, 1980), but some have two or more generations per year. Wolters (1983) found, in the collembolan population of a German beech-wood on limestone, the following numbers of generations for non-univoltine species:

Bourletiella bicincta 2,
Folsomia quadrioculata 2,
Isotoma notabilis 3,
Isotomiella minor 3,
Megalothorax minimus 3–4,
Orchesella flavescens 1–2,
Tullbergia krausbaueri 2.

However, in many cases it is difficult to evaluate the life cycle of Collembola by analyzing the temporal distribution of size classes, because body size depends on abiotic factors and the availability

of food, and the period of reproduction may cover a longer time interval (Healey, 1971), thus making separation of different generations less obvious. This variable pattern of body-size distribution is even typical for univoltine populations: an example is *Tomocerus flavescens* (Fig. 6.6; Wolters, 1983).

Oribatid mites have long developmental times in comparison to Collembola. The results of a study of the oribatids in a Danish beech forest suggest that many mites, although initiating between one and three generations a year depending upon species, may take a year or more to complete development from egg to sexually mature adult (Luxton, 1981b, d).

Phytophagous insects. Most species that develop in the vegetation layer are univoltine — for instance the weevil *Rhynchaenus fagi* (Bale and Luff, 1978). The life-history patterns of phytophages are often correlated with the pattern of nitrogen levels or the concentration of secondary plant compounds in the plant material (see p. 79). A large proportion of temperate zone Lepidoptera feed as larvae partially or entirely on young, spring plant growth. In particular, many obligately univoltine, arboricolous species feed entirely in spring, overwintering as partially grown larvae which complete feeding the following spring (Schweitzer, 1979). Multivoltine insects are faced with food supplies of severely declining quality (see p. 97). This is probably the primary factor in forcing many species into univoltinism with larval feeding largely in spring. Deciduous trees exhibit seasonal variation in the production of new leaves. Trees of the "*Quercus*-type" (such as *Quercus robur* and *Prunus padus*) produce new leaves mainly in spring, while new foliage in trees of the "*Populus*-type" (such as *Populus*, *Betula*, *Alnus*) is also produced late in the season. Consequently, the proportion of specialists among Finnish macrolepidopteran larvae was significantly higher in spring on trees of the *Quercus*-type, while on the *Populus*-type the proportion of specialists was more constant over the seasons (Niemelä, 1983).

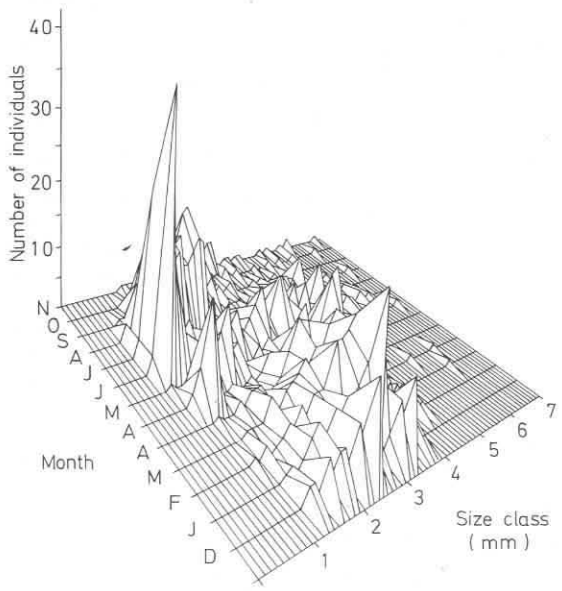


Fig. 6.6. Life cycle of *Tomocerus flavescens* according to the distribution of size classes. The number of individuals refers to 12 soil–litter samples with a diameter of 22 cm. Modified from Wolters (1983).

Spiders. Araneida have a variety of life cycles, ranging from extreme eurychrony[1] to stenochrony[1] (Schaefer, 1976, 1977). There are no life-history patterns typical for forest species (Schaefer, 1976). Species of the vegetation layer tend to be univoltine, while many other spider species in forests are biennial (Schaefer, 1976; Toft, 1976, 1978; Albert, 1982). Life-history patterns of spiders in a Danish beech forest — and probably in other forests, too — showed greater similarity within the different strata than between them (Toft, 1976, 1978).

Parasitoids. The majority of parasitic Hymenoptera are univoltine. A temporal sequence of host colonization characterizes forest canopies. Specialist parasites enter the community early in the season, followed by polyphagous parasites as the community becomes more diverse (Askew, 1975; Askew and Shaw, 1979). For parasitoids of Cynipidae causing oak galls and of deciduous-tree leaf miners, seasonal changes in species composition are almost always the result of addition of species; rarely do they result from a parasite's

[1]Eurychrony: activity and period of reproduction during several seasons of the year (adj. eurychronous); stenochrony: period of reproduction during a definite season of the year (adj. stenochronous).

completion of development and departure from the community as an adult before the time when the gall or mine would be fully developed (Askew, 1980).

Some general patterns emerge concerning life cycles of invertebrates in temperate deciduous forests:

(1) Populations in the higher strata tend to be stenochronous. The majority of the species are univoltine.

(2) Animal species in the soil and litter layer tend to be more eurychronous and often are either plurivoltine, or have a longer life span of two to several years.

(3) Life cycles seem to be more similar within the strata than between different strata.

(4) Changes in the composition of the communities during the season are effected rather by the addition of new populations than by exchange of species, some of which may retire to a resting stage (such as egg or pupa).

Hibernation and winter activity

During winter, temperatures in the litter and soil rarely fall below 0°C — sometimes during spells of severe frost without a protective snow cover. There are different kinds of adaptations of invertebrates to the cold winter period (Schaefer, 1976, 1977): migration to lower strata of the soil–litter subsystem; migration to sheltering microhabitats, such as leaf litter, grass tussocks or tree stumps; lowering of the supercooling points; hibernation in a resistant developmental stage (depending on the microclimate of the hibernaculum, Fig. 6.7); or winter activity.

Feeding activity ceases at a temperature threshold typical of the particular soil and litter groups. This helps to decrease the supercooling points, because the gut is emptied and does not contain particles as possible crystallization nuclei for freezing. The rate of decomposition certainly is affected by the limitation of feeding activity. For example, *Glomeris marginata* as a primary decomposer eats very little during winter. *Glomeris* begins to feed and migrate upwards in the soil when the daily mean temperature of its surroundings reaches 5.5 to 6.3°C (Bocock and Heath, 1967).

Winter activity. Typical winter-active animal species in the litter layer include spiders, Collembola,

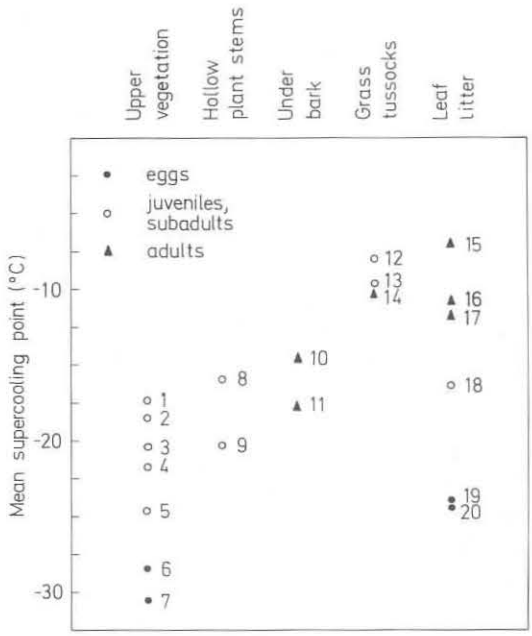


Fig. 6.7. Supercooling points of spiders (Araneida) overwintering in beech forests in Schleswig-Holstein (Northern part of West Germany). *1*: *Linyphia peltata*, *2*: *Tetragnatha montana*, *3*: *Araniella cucurbitina*, *4*: *Theridion pallens*, *5*: *Philodromus aureolus*, *6*: *Drapetisca socialis*, *7*: *Floronia bucculenta*, *8*: *Gongylidium rufipes*, *9*: *Erigonidium graminicola*, *10*: *Segestria senoculata*, *11*: *Marpissa muscosa*, *12*: *Bathyphantes nigrinus*, *13*: *Euophrys frontalis*, *14*: *Pachygnatha listeri*, *15*: *Macrargus rufus*, *16*; *Lepthyphantes cristatus*, *17*: *Microneta viaria*, *18*: *Linyphia hortensis*, *19*: *Metellina segmentata*, *20*: *Linyphia triangularis*. Modified from Schaefer (1977).

Staphylinidae and larvae of Diptera (Schaefer, 1976, 1977, 1983a; Aitchison, 1983; Joosse, 1983; Hövemeyer, 1984). Other invertebrate species may also be active in winter: earthworms, snails and slugs, myriapods, other beetles. However, their general level of activity is low.

Winter-active arthropods feed at low temperatures. Aitchison (1983) observed that hemiedaphic winter-active Collembola could feed on fungi at temperatures down to −2.5°C in southern Canada. The preferred food appeared to be fungi of the family Dematiaceae. Feeding of dipterous larvae was highest in autumn and winter in a German moder beech forest (Altmüller, 1979).

Aestivation

The activity of invertebrates in litter, and some soil-dwelling populations (for instance, earthworms, slugs, Collembola) decreases during sum-

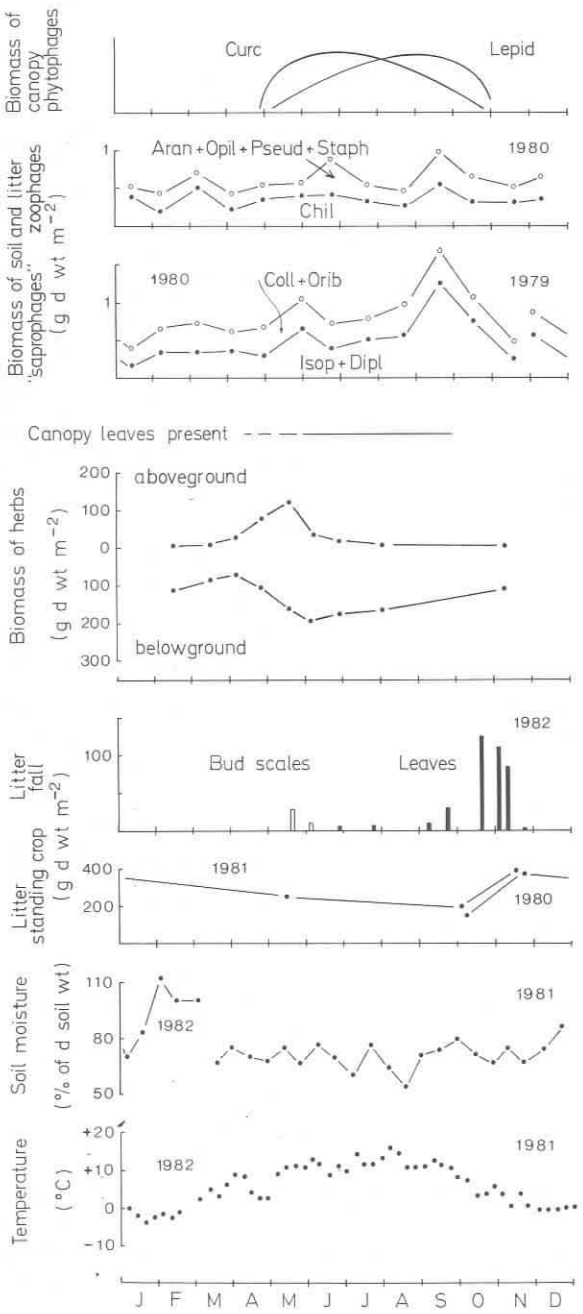


Fig. 6.8. Seasonality in a beech-wood on limestone (Göttinger Wald). Soil moisture and biomass of canopy arthropods are indicated diagrammatically. Curc: Curculionidae, Lepid: Lepidoptera, Aran: Araneida, Opil: Opilionida, Pseud: Pseudoscorpionida, Staph: Staphylinidae, Chil: Chilopoda, Coll: Collembola, Orib: Oribatei, Isop: Isopoda, Dipl: Diplopoda. Based on partly unpublished data from J. Schauermann and R. Hartmann (temperature), R. Aldag (soil moisture), Andres and Becker (1982) (litter standing crop), P. Pellinen and H. Kramer (litterfall), W. Schmidt (herb biomass), R. Strüve-Kusenberg (biomass of Isopoda), T. Sprengel (biomass of Diplopoda), Wolters (1983) (biomass of Collembola), H.-D. Baaske (biomass of Oribatei), M. Schaefer (biomass of zoophages).

mer droughts. This correlates with decreasing rates of decomposition in the middle of summer.

Seasonality and the ecosystem

Temperate deciduous forests are characterized by drastic seasonal changes in the availability of resources, especially those associated with the canopy microhabitats. This seasonality is one of the reasons that there is no permanent canopy subsystem based on branches, twigs and leaves as resources (Carroll, 1979).

Most plant and animal life begins early in the spring, because the litter layer is warmed by solar radiation to temperatures well above 30°C in comparison with the naked soil beneath the litter (Tischler, 1984). In a succession of ecological events in a beech forest in Denmark, there is no ecological hiatus between spring and summer, nor between summer and autumn, to substantiate a four-season concept (Nielsen, 1974). However, the considerable number of temporally predictable ecological events observed in a beech forest suggests, if anything, a concept of an annual cycle subdivided into several phenophases.

Some of the seasonally changing parameters are depicted for a German beech-wood in Fig. 6.8. They suggest some possible interrelationships: the period of aestivation of the mesofauna in response to summer drought; development of canopy arthropods in response to appearance of canopy leaves; and, in advance of the new litterfall, peaks of predator biomass shortly after the maxima of mesofauna biomass.

Ecosystem processes are closely linked to seasonal changes in the food resources that provide energy and elements (Cousens, 1974). According to a simple model, the animal species of higher trophic levels cannot become very active or abundant until their food resources have become plentiful. The main growth period for autotrophs is spring and early summer; of herbivores, late spring and summer; of predators, summer; of decomposers, summer and autumn. However, there is the danger of oversimplification. For example, in the herbivore–plant subsystem second-

ary plant substances may act as modifiers. Litter often is consumed only after a period of weathering (see Chapter 9). The input of resources for saprophages is not as discontinuous as often supposed. Small non-leafy materials, such as flowers, bud scales, insect frass etc., fall in the early spring and summer (Nielsen, 1977/78) and often contain high levels of nutrients. In a study by Carlisle et al. (1966), non-leaf materials contained 29.9% of the nitrogen, 40.2% of the phosphorus and 25.2% of the potassium of all types of litter, although these materials accounted for only 14.7% of the dry weight of total litter. This input of high-quality litter should be taken into account in investigations of seasonal variations in activity of micro-organisms and animals in the soil.

SUCCESSION

Macrosuccession

Most natural succession in deciduous forests begins with a gap opening in the canopy, as trees die of old age, from pests and diseases, from fire, or from lightning. A large tree falling may bring others down, forming an extensive glade. Another type of secondary succession begins with clear-felling of a larger area.

Reviews of macrosuccession as a process have been given by Odum (1971) and Horn (1974, 1981). Standing crop increases, and within a relatively short period maximum productivity is attained. Litterfall increases during early years of succession, reaches a peak, and then decreases with age (O'Neill and DeAngelis, 1981). Decomposition is less than net production during the development of a forest. Consequently the number of decomposers is lower than in mature stands. Often species diversity reaches maximum values during intermediate phases of succession (Horn, 1974).

Usher et al. (1982) have reviewed the structure of successional soil fauna communities and emphasized that "early" and "late" successional communities of Collembola are quite distinct, a phenomenon which could be caused by indirect influences of the vegetation cover or by competitive relationships favouring species with a *K*-strategy[1] in later stages of succession.

There seems to be a good correlation between the turnover of plant-inhabiting animal species and changes in vegetation structure ("physiognomic turnover") along the sere, regardless of the plant species turnover. Southwood et al. (1979) followed changes in the diversity of Coleoptera and Heteroptera (including both phytophagous and predatory species) along a secondary succession in southern England. Up to a successional age of 16 months, taxonomic diversity of plants and insects both increased. Thereafter, plant species diversity fell. Insect diversity also decreased, but much less than plant diversity, probably because insect diversity was maintained by the high structural diversity of the plants later in the succession. A correlation between the number of insect species and the structural complexity of vegetation (including measures of spatial complexity, that is size and growth forms, and resource diversity) across four successional stages from ruderals to woodland was very high ($r^2 = 0.87$). Spatial complexity alone accounted for less of the variation in insect species richness ($r^2 = 0.71$). There was no correlation, over the succession as a whole, between plant species diversity and insect species diversity.

Clear-cutting

Clear-felling greatly increases the amount of organic matter on the ground. This material subsequently decreases (for instance, in a North American hardwood forest by 3.07 kg m^{-2} during 15 years: Covington, 1981), and then increases again. The ground flora drastically changes after cutting.

Among the macrofauna the response of the carabid beetles has been well studied. Knie (1975) found that, in a German mixed deciduous woodland, the number of carabid species was highest in clearings, but population densities were low. Many forest species migrated into clearings, while clearing species avoided the forest. After clear-cutting

[1] *r*-strategy: within the concept of *r*–*K*-selection an ecological strategy of a species in variable or unpredictable environments, typically with small body size, rapid growth, short life span, efficient dispersal and devotion of a large proportion of energy to the production of offspring; *K*-strategy: an ecological strategy of a species in relatively constant or predictable environments, typically with larger body size, slow development, late reproduction, relatively high competitive ability and devotion of a smaller proportion of energy to the production of offspring.

the within-genus component of carabid species diversity increased significantly (Lenski, 1982).

Hill et al. (1975) stated that the densities of the mesofauna decrease after cutting and slowly return to normal after a number of years. In a hardwood catchment in the southern Appalachians (U.S.A.), clear-cutting caused a reduction in numbers of oribatid mites and a shift to smaller forms (Abbott et al., 1980; Seastedt and Crossley, 1981). Karppinen (1957) reported a temporary increase for a Finnish forest, followed by a long-period decline. Huhta (1976) attributed this response solely to food availability. Debris from cutting temporarily increases food abundance; afterwards litter production and the standing crop of organic matter decline. Even though cutting greatly increased organic matter at the site in the southern Appalachians, the oribatid fauna was unable to exploit this resource. The immediate drop in densities probably resulted from lethal or near-lethal temperatures on the litter and soil surface (Abbott et al., 1980). In soil strata below −5 cm densities of microarthropods increased, primarily as a result of increased abundance of prostigmatid mites (Seastedt and Crossley, 1981).

Role of phytophages

Herbivorous mammals may channel succession into particular directions by selective feeding. In most cases the animals retard succession. Deer and other browsers often prevent the establishment of shade-tolerant understorey trees or delay the establishment of any trees at all. Thus, succession may be arrested in a "grazing climax" at the grass stage or in a "browsing climax" at the shrub stage (Richardson, 1977), especially in the western fringes of the deciduous region in North America.

On the other hand, insect herbivores may accelerate the series of transformations from plant communities with smaller biomass and higher nutrient/light requirements (Schowalter, 1981). Thus insects may regulate ecological succession by altering plant competitive relationships. Sites with reduced insect herbivore abundance should show slower rates of plant species replacement. An example is the system *Prunus pennsylvanica* (pin cherry) — *Malacosoma americanum*. This phytophagous species contributes to reduced importance of the pin cherry in older forests (Schowalter, 1981).

According to Feeny's (1976) "apparency theory", early successional plants have an increased palatability (Cates and Orians, 1975). This was confirmed by Reader and Southwood (1981), although these authors found considerable variations within plant communities and between herbivores. Experiments with the slugs *Ariolimax columbianus* and *Arion ater*, which are generalized herbivores, fed with 100 plant species of three growth forms and from different seral stages, indicated that early successional annuals were significantly more palatable than early successional perennials, which were significantly more palatable than later successional species (Cates and Orians, 1975).

Animals and nutrient cycles

Mature forests tend to have nutrient cycles which are more closed than those of earlier successional stages, with rates of internal nutrient cycling greatly exceeding nutrient input and output (Bormann and Likens, 1981). However, earlier successional forest ecosystems tend to be more nutrient-conservative than climax stages where cycling of nutrients is more efficient (Gorham et al., 1979). Are animals involved in these processes? The influence of the microflora (which in turn is affected by the soil and litter fauna, see Chapter 9) is indisputable. After a disturbance, nutrients are mobilized, probably favoured by litter temperatures which are *c.* 10°C higher in exposed soils than under plant canopies. Later in succession the ratio of carbon to mineral nutrients in woody material is usually high, and immobilization of nutrients by microflora in and around this rich carbon source can significantly decrease the rate of element escape to ground-water and streams (Gorham et al., 1979). Rice (1974) suggested that plants characteristic of "mature" ecosystems produce allelochemic substances which suppress nitrification, thus leading to the retention of nitrogen (as NH_4^+). On the other hand, early successional systems produce smaller amounts of inhibitory substances, and have higher rates of nitrification and element losses.

Microsuccession

Colonization of freshly fallen litter constitutes an important type of microsuccession. Wide-

spread, distinct microseres in temperate deciduous forests also occur in dead wood.

Colonization of leaf litter

Attention has focused on the succession of fungi on decomposing leaf litter fallen from the canopy onto the forest soil surface. Summaries have been given by Jensen (1974), Swift (1976), Hayes (1979) and Kjoller and Struwe (1982). The parasitic fungi of the phylloplane — the surface of the living leaf — may persist as active decomposers for considerable time after the death of the host tissue (Swift et al., 1979). Parasites give way to primary saprophytes (utilizing simple carbon compounds) on the senescent leaf and then to secondary saprophytes (utilizing cellulose and lignin) on the now-dead leaf. Finally, soil-inhabiting fungi colonize the litter (Swift, 1976; Hayes, 1979; Parkinson, 1983). Hudson (1968) postulated that this three-stage succession characterizes the degradation of plant litter. Kjoller and Struwe (1982) have critically examined the concept of fungal succession, and concluded that the idea of stepwise utilization of the litter components in order of increasing complexity is too simple, because many fungi exhibit "mixed function" in their utilization of simple and more complex carbohydrates.

De Boois (1976) analyzed the succession of fungi on oak (*Quercus petraea*) leaves for three years by means of monthly isolations on cherry agar from washed leaf material. In the first phase of colonization *Aureobasidium pullulans* is the presumptive cellulose decomposer in litter of low pH. Furthermore, a *L*-layer Basidiomycete, which in pure culture causes a weight loss of 20% in five months, is active during the first months after leaf fall. This species clearly prefers the freshly fallen litter to older material. The soil inhabitants colonize the leaf as early as six months after leaf fall. *Morteriella ramanniana*, *M. isabellina*, *Penicillium* and *Trichoderma* spp. were found to be the most important. The entire succession fits the scheme of Hudson (1968). Soil-inhabiting fungi do not contribute greatly to direct decomposition of the leaf litter. These species presumably grow mainly on dissolved substances originating from leaching and from the decomposition by other microorganisms.

How does the litter fauna invade the freshly fallen litter, using the dead plant material and/or the fungal hyphae as food? Anderson (1975a) monitored the successional development of soil animal communities associated with leaves of beech (*Fagus sylvatica*) and chestnut (*Castanea sativa*). Representatives of most groups of soil animals (enchytraeid worms, dipterous larvae, Collembola, mites) colonized the litter bags within the first few weeks in the field; there were no "pioneer species". The soil animal populations were qualitatively and quantitatively similar in the two species of litter despite marked differences in decomposition rate of beech and chestnut litter. Obviously the soil animal populations were governed by non-nutritional properties of the litter. Species of oribatid mites changed, but only slightly; the 12 most abundant species were present in the bags throughout the study. In the first phase of succession the oribatid mites apparently had a high proportion of fungal material in their guts.

Hagvar and Kjondal (1981) detected five clear phases in the succession of microarthropods in decomposing birch leaves during a three-year study in a clear-cut area of a Norwegian coniferous forest: (1) immediate immigration, with pioneer species predominating, but with the majority of all species recorded from the bags over the three years being present; (2) increase of diversity and of the proportion of species typical of deeper layers; (3) invasion of the substrate by additional rare species; (4) reduction in abundance of most species, but with practically no changes in species composition; (5) reduction of abundance and species number after complete exploitation of the resources. Analysis of gut contents showed that almost all pioneers were typical microphytophages. They ingested large amounts of fungal spores in the early phase, with fungal hyphae becoming increasingly important later.

Streit and Roser-Hosch (1982) observed that compost cylinders 75 cm high filled with a mixture of cattle manure and corn straw, and exposed in a beech forest, were colonized relatively quickly by Arthropleona (Collembola), whereas colonization by the Cryptostigmata was much slower.

Microsere in dead wood

The succession of biota in dead wood is reviewed by Dajoz (1974), Käärik (1974), Swift (1977) and Martin (1979). Communities of animals associated with dying and dead wood were described by Elton

(1966). Swift (1977) recognized several successional stages in the microbial and faunal community of dead wood: (1) the colonization stage, dominated by fungi (mainly Basidiomycetes), bacteria and bark beetles; (2) the decomposition stage, characterized by exploitation by fungi (dominant white-rot and brown-rot Basidiomycetes) and invasion by wood borers (mainly beetles such as Anobiidae, Cerambycidae and Scolytidae, and Hymenoptera such as Siricidae); (3) the terminal stage, characterized by soil fungi and bacteria; general litter and soil animals like Collembola, mites, Enchytraeidae; and the larger Diplopoda, Isopoda, dipterous larvae, gastropods and earthworms, which ultimately enter the log through the bore holes, followed by predators such as staphylinid beetles or Diptera. Of the branches on the forest floor in an English abandoned beech and coppiced oak woodland, 60% showed signs of past and present animal activity (Swift et al., 1984). Diptera were the dominant group, Tipulidae being the most prevalent family (*Tipula flavolineata* was detected in 39% of the branches). Further prevalent species were *Cylindroiulus punctatus* (Diplopoda), *Cylindronotus* sp. (Coleoptera), *Lithobius variegatus* (Chilopoda), *Lumbricus rubellus*, *L. terrestris* (Lumbricidae) and *Oniscus asellus* (Isopoda). Branches invaded by animals were generally more decayed than uninvaded branches on the ground which in turn were more decayed than branches at fall (Swift et al., 1984).

Fog (1977), in analyzing the microflora of beech stumps, found that breakdown was accomplished by white-rot rather than brown-rot fungi (see Chapter 9). The surface plane was first colonized by yeast cells. After three to six months these were replaced by a very diverse flora of bacteria and microfungi. After a few waves of colonization by different fungi, the microflora gradually stabilized and then remained relatively unchanged. Amounts of hyaline hyphae were high the first one to two years and then declined, whereas amounts of bacteria and dark brown hyphae increased as the stump aged.

TROPHIC RELATIONSHIPS

Forest animals belong to different feeding types. Main categories are herbivores (phytophages), detritivores (saprophages including microphytophages feeding on microfloral populations) and carnivores (zoophages). A minority of species are "omnivorous" (pantophagous), such as *Arion ater* (Jensen, 1975) or larvae of Elateridae (Schauermann, 1986). The role of animals as consumers in energy flow, decomposition and nutrient dynamics is dealt with in Chapter 9. Ecological problems concerning animals and their food resources include questions of foraging strategy, degree of specialization, and interactions between consumers and food items.

In many cases feeding types are only rough categories, and the assignment of species to definite trophic levels is not possible. Examples are snails and slugs (M. Corsmann, pers. comm., 1986) (Fig. 6.9), nematodes, oribatid mites (Anderson, 1975a) (Fig. 6.9), Carabidae, dipterous larvae, birds and small mammals.

Oribatids are principally fungivorous (Wallwork, 1983), although a number of species are known to consume the decaying leaves of higher plants (Hartenstein, 1962; Luxton, 1972; Wallwork, 1976, 1983) (cf. Fig. 6.9). Rockett (1980) observed even nematophagy in *Pergalumna* and other oribatids, which are mainly saprophagous and/or microphytophagous. However, according to Schuster (1956), oribatid mites only rarely feed on living or dead animals.

Woodland gastropods can feed on living or dead material of higher plants (cf. Fig. 6.9). Analyses of the faeces of seven species of woodland, litter-dwelling snails showed that all feed predominantly on living or dead material of higher plants. *Trichia striolata* and *Arianta arbustorum* took more chlorophyll-containing plant material than the other species. *Discus rotundatus* had a significant amount of fungus in its faeces, while the faeces of *Oxychilus cellarius* and *O. alliarius* contained a significant amount of animal material (Mason, 1970). Some species on tree stumps do not feed on algae, as is commonly assumed, but on bacteria (Fog, 1979b).

Various attempts have been made to classify soil nematodes into nutritional types (Yeates, 1971). Distinctions have been made between predators, microbial feeders, omnivores and plant feeders. However, these categories are rarely exclusive. Soil nematodes are so ecologically plastic that few species have specialized feeding habits (Wallwork, 1976).

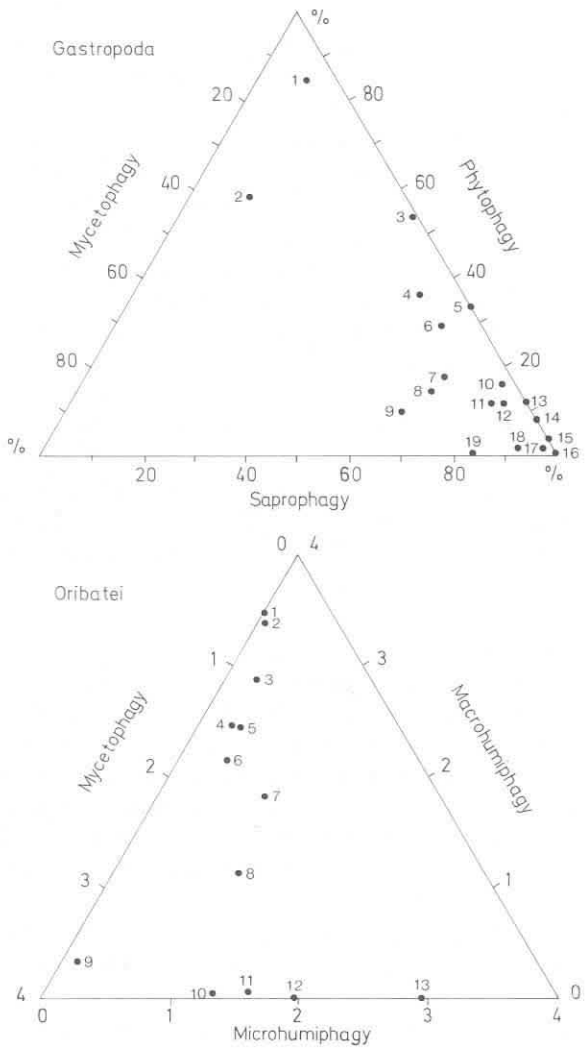


Fig. 6.9. Food preference of Gastropoda (in a beech-wood on limestone, "Göttinger Wald"), based on unpublished data from M. Corsmann, and of oribatid mites from a sweet chestnut–beech forest, according to data from Anderson (1975a). Values for Gastropoda are given as percentages for higher plant material (green), fungal hyphae and litter. Values for Cryptostigmata (=Oribatei) were obtained by scoring gut contents [plant material (macrohumiphagy), amorphous material (microhumiphagy), fungal material] according to a series of quartile grades from 0 to 4.

Gastropod species (top): *1*: *Lehmannia marginata*, *2*: *Malacolimax tenellus*, *3*: *Ena montana*, *4*: *Cochlodina laminata*, *5*: *Iphigena plicatula*, *6*: *Trichia hispida*, *7*: *Arianta arbustorum*, *8*: *Arion rufus*, *9*: *Helicodonta obvoluta*, *10*: *Perforatella incarnata*, *11*: *Aegopinella nitidula*, *12*: *Arion circumscriptus*, *13*: *Discus rotundatus*, *14*: *Azeca menkeana*, *15*: *Carychium tridentatum*, *16*: *Vitrea crystallina* and *Aegopinella pura*, *17*: *Oxychilus cellarius*, *18*: *Laciniara biplicata*, *19*: *Ena obscura*.

Oribatid species (bottom): *1*: *Phthiracarus ligneus*, *2*: *Steganacarus magnus*, *3*: *Liacarus xylariae*, *4*: *Adoristes ovatus*, *5*: *Hermanniella granulata*, *6*: *Nothrus sylvestris*, *7*: *Nanhermannia elegantula*, *8*: *Platynothrus peltifer*, *9*: *Eniochthonius minutissimus*, *10*: *Chamobates cuspidatus*, *11*: *Carabodes labyrinthicus*, *12*: *Tectocepheus velatus*, *13*: *Oppia* spp.

Phytophagy

Rhynchota, Coleoptera, Lepidoptera and Diptera are typical and important phytophagous taxa in temperate deciduous forests. Nematodes may be important in consuming roots. Compared with grassland communities, deciduous forests contain remarkably few grazing and browsing mammals, and also few seed-eating birds (Richardson, 1977). Feeding relationship between animals and trees may be categorized as: phyllophagy, sap-feeding on leaves and roots, xylophagy (by wood-borers or bark borers), rhizophagy and seed predation. The phyllophagous arthropods include ectophagous species, leaf miners, and gall-inducing species.

Degree of specialization

Many herbivorous insects on trees are monophagous. The leafhopper subfamily Typhlocybinae may be taken as an example, as it is a typical wood-inhabiting group (56 out of 88 species in Britain are associated with tree or shrub species [Claridge and Wilson, 1976]). Typhlocybinae on trees are specialized to a much larger extent than in grassland communities. Of 31 woodland species studied by Claridge and Wilson (1976), 16 were regarded as monophagous, 12 as oligophagous and 3 as polyphagous. For some species Claridge and Wilson (1978) demonstrated that nymphs were able to use a wider range of plants as food, and to survive on them, than the food plant ranges observed in the field. Probably oviposition behaviour in these insects is discriminatory and leads to the observed field distributions. Among tree-associated woodland leafhoppers, there is now considerable evidence to suggest that both oviposition preference and detailed behaviour patterns involved in oviposition are species-specific, inherited characteristics (Claridge and Reynolds, 1972). It can be speculated that trees, as large units of habitat, keep insects during their short-range flights in contact even with the same individual plant (Claridge and Wilson, 1976). In addition, woodlands are relatively permanent habitats. Complete life cycles may take place

entirely in them, and even on one individual tree. All known tree-feeding leafhoppers lay eggs in their food plants.

However, it is sometimes difficult to determine the degree of specialization or generalization. Even so-called monophagous species may have a wider diet than presumed. For example, individuals of winter-starved *Rhynchaenus fagi* prefer young beech (*Fagus sylvatica*) leaves to an alternative plant (Bale and Luff, 1978); but in the absence of beech other plants are eaten, and may be important under field conditions. Newly emerged weevils in June and July are likely to feed to a limited extent on plants other than beech, and were observed to prefer raspberry (*Rubus idaeus*) to the youngest available beech leaves. Furthermore, the age of the food resources is important — for instance, in spring *R. fagi* prefers young beech to 5-week-old beech leaves (Bale and Luff, 1978).

Secondary plant substances may influence host selection. For example, the galling aphid *Pemphigus betae* does not induce galls at random on leaves of its host plant, *Populus angustifolia*. Probability of stem mother success in forming a gall, body mass of stem mother and progeny, number of progeny, developmental rate of progeny to maturity, and numbers of embryos in mature progeny are all correlated positively with leaf size at maturity (Whitham, 1978). Leaf size at maturity is predictable from leaf position in the shoots at bud burst. A strong inverse relationship has been established between the concentration of total phenol glycosides and the suitability of a tree, a leaf, or leaf section for galling at the time of bud burst, when the colonizing stem mothers are at the peak of their activity. Expanding leaves within the same shoot have different phenol concentrations; the potentially largest leaves have lower phenol levels, suggesting that phenol concentrations play a role in leaf selection (Zucker, 1982).

According to Cates (1980), herbivores with restricted diets tend to prefer young, nutritious and highly toxic leaf material, whereas more polyphagous herbivores often prefer mature leaves, which are less nutritious, but are generally lower in toxic substances.

Plant–animal interactions

Plant species and associated phytophagous animals form a system in which the populations interact over both ecological and evolutionary time. Studies of relationships between plants and animals (primarily insects) have led to four conclusions: (1) animal phenology and population dynamics are often influenced by host-plant defences (Cates, 1980; Haukioja, 1980; Mattson, 1980); (2) animals potentially have an effect on the population dynamics of plants — for instance, by seed predation, seed dispersal or pollination (Harper, 1977); (3) herbivores change the competitive relationships among plants through selective herbivory (Whittaker, 1979), often accelerating or slowing down the rate of ecological succession (Connell and Slatyer, 1977) and increasing plant species diversity (Janzen, 1970); (4) herbivores influence the rate and direction of nutrient flux between vegetation and litter (Springett, 1978; Schowalter et al., 1981, 1986). Several aspects of these generalizations are discussed below.

Defoliation

Phytophagous insects may consume foliage, sap, woody tissue or reproductive organs, thereby affecting primary production, mainly wood growth. Foliage consumption is the most harmful stress. The consequences of almost complete defoliation are reviewed by Franklin (1970), Rafes (1970), Kulman (1971), Heichel and Turner (1976) and Harper (1977).

Severe defoliation of deciduous hardwoods by insects may reduce the radial growth of the stems, and repeated defoliation may increase mortality (Heichel and Turner, 1976, 1984; Crawley, 1983). Defoliation injures trees by reducing photosynthesis and by interfering with transpiration and translocation of food, and in some cases cancels competitive advantage in respect to the biotic environment (Franklin, 1970). According to Rafes (1970) increment losses are insignificant until defoliation exceeds about 75% of the photosynthetic biomass. A defoliator that takes only young leaves harms the plant more than one that consumes only old and senescent leaves. Haukioja and Niemelä (1974) found, for instance, that *Oporinia autumnata*, was more destructive to birch than *Dineura viridiorsata*, because the former feeds earlier and grows more rapidly. Large-scale defoliation of plants in natural communities by invertebrates seems to be comparatively rare (Hairston et al., 1960). Some well-studied examples

are the virtually complete defoliation of mountain birch (*Betula tortuosa*) in parts of northern Finland by the autumnal moth *Oporinia autumnata* (Tenow, 1972), and heavier intensities of defoliation by the forest tent caterpillar, *Malacosoma disstria*, in aspen (*Populus*) forests in North America (Franklin, 1970).

Partial defoliation can increase photosynthetic efficiency of the remaining leaves and stimulate the development of dormant buds and increase branching (Harper, 1977), thereby not necessarily causing a reduction in net plant growth. Generally deciduous hardwoods are particularly adept at surviving severe and repeated defoliations (Heichel and Turner, 1976). Oak (*Quercus* sp.) can withstand repeated defoliation of the primary growth through the production of lammas shoots (Gradwell, 1974). However, there is no evidence that the principal function of lammas shoots is in compensation for herbivore feeding (Crawley, 1983). Heichel and Turner (1976) studied the phenology of bud-break and the leaf growth of manually defoliated and undefoliated red oak, *Quercus rubra*, and red maple *Acer rubrum*. After partial defoliation the foliage re-grew. The leaf area of regrowth was lower than the original area — for instance, oaks after complete defoliation had 39% and maples 33% of control values. The leaves contained less total sugars and less starch, but the nitrogen content was unaffected. Complete defoliation had previously been observed to elicit foliage regrowth in other tree species, such as sugar maple, *Acer saccharum*; yellow birch, *Betula alleghaniensis*; ironwood, *Carpinus caroliniana*; quaking aspen, *Populus tremuloides*; basswood, *Tilia americana*; and elm, *Ulmus americana* (Heichel and Turner, 1976). Deciduous trees are thus frequently stimulated to regenerate their leaf canopy following defoliation. However, Heichel and Turner (1984) observed that defoliation reduced branch growth more than leaf production in *Quercus rubra* and *Acer rubrum*. Three years of successive 50, 75 and 100% leaf removal treatments reduced the mean lateral plus terminal branch growth by 40% in red oak and by 23% in red maple.

Anti-herbivore defences

There are many excellent summaries on anti-herbivore defences of plants (for instance, Hanover, 1975; Harborne, 1978; Rosenthal and Janzen, 1979; Edwards and Wratten, 1980; Crawley, 1983; Strong et al., 1984; Schowalter et al., 1986). Different patterns of defence by deciduous trees are apparent: (1) escape in space and time, (2) low nutritive value of plant tissue, (3) accumulation of defensive secondary plant substances, (4) wound-induced chemical mechanisms, (5) early fall of leaves, (6) compensatory plant growth.

(1) **Escape in space and time**. "Short-lived" plant tissues (such as annual herbs) escape from their herbivores in space and time to a larger extent than do more predictable plant tissues. This is especially true for young leaves of deciduous trees. Examples are the systems of oak (*Quercus* sp.)/winter moth (*Operophthera brumata*) and *Quercus robur*/*Tortrix viridana* (Rhoades and Cates, 1976). Intrapopulation variability in phenology is an evolutionary response of the plant. In natural stands of oak and other trees, bud-burst may range over ten or more days (Feeny, 1970) making it difficult for the herbivore to synchronize precisely with every tree in the population. Witter and Waisanen (1978) found a very significant linear relationship between the mean proportion of trembling aspen (*Populus tremuloides*) buds infested by tortricid caterpillars (primarily *Choristoneura conflictana* and *C. rosaceana*) and the mean flushing date of tree clones. Early-flushing clones had significantly higher population levels of tortricid caterpillars (18%) than the late-flushing clones (3%). Whitham (1981) hypothesized that genetic variability of individual host trees is an adaptive response to herbivory. Trees as heterogeneous environments are mosaics of varying susceptibilities to herbivore attack.

(2) **Low nutritive value of plant tissue**. One defence of "apparent" plants (see below) is a low level of nitrogen (McNeill and Southwood, 1978). Young foliage has a higher nitrogen concentration (Feeny, 1970). Feeny (1976) and Rhoades and Cates (1976) considered young foliage to be an ephemeral resource ("a phenological window", Feeny, 1976) for insects requiring nitrogen-rich food during their growth. According to Schweitzer (1979) early batches of Noctuid larvae of the subfamily Lithophaninae feeding on leaves of trees had significantly greater weights than late batches, and had significantly higher rates of survival. Wint

(1983) found that available, rather than total, leaf protein levels were related to the performance of winter moth (*Operophthera brumata*) larvae.

However, Moran and Hamilton (1980) assume that individual plants do not necessarily benefit by possessing traits which lower herbivore fitness by lowering the nutritive quality of plant resources. Herbivore damage could increase because herbivores on an "adapted" plant, in order to obtain minimum nutritional requirements, might consume more leaves than would be the case if nutritive quality were high.

(3) **Accumulation of defensive secondary plant substances**. Coevolutionary arguments have led to the hypothesis that a plant's investment in chemical defence is related in both quantitative and qualitative terms to its "apparency", that is exposure to herbivores in time and space (Feeny, 1976). This author termed long-living plants "apparent", since they are easily found by herbivores and are unlikely to escape predation. These plants adopt defences such as low nitrogen content, low water content, and high concentrations of tannins and other secondary plant substances, which are generally repellent to most feeders. By contrast, herbs with a short life cycle are "unapparent", since they can more easily escape being fed upon. Their chemical defence is thus more likely to involve the production of specialized chemicals (such as alkaloids or glucosinolates) which are produced in small quantity and which generalist herbivores cannot readily detoxify. Usually the nutritional quality of canopy leaves decreases during the vegetation period, and is correlated with increasing tannin levels. Larvae of herbivorous caterpillars (9 species of Papilionidae, 9 species of Saturniidae, the bombycid species *Bombyx mori* and the noctuid species *Spodoptera eridania*) grew faster and more efficiently on herbaceous plants than on foliage of shrubs and trees (Scriber and Feeny, 1979).

However, according to Bernays (1981) there is as yet no unequivocal proof of an antidigestive effect of tannic acid or of condensed tannins in insects. Increased tannin content of leaves is commonly associated with increased hardness, reduced nitrogen and water content, and perhaps a variety of other factors. Haukioja et al. (1978) have shown a negative correlation between growth of *Trichiosoma lucorum* (Cimbicidae) and of *Dineura viridi-dorsata* (Tenthredinidae) and leaf tannin content of birch (*Betula pubescens* subsp. *tortuosa*) throughout two growing seasons. However, much greater changes in the nitrogen content occurred concurrently, while moisture level also dropped over the same period from 73 to 57%. Faeth (1985) found no consistent pattern of correlations between seasonal changes in tannin and protein content of oak (*Quercus emoryi*) and the degree of herbivory.

Tannins can adversely affect predators of the herbivores, such as tits (Perrins, 1979). The caterpillars collected by the tits contain large quantities of leaf material in their gut and so the young tits must also consume fairly large quantities of oak-leaf tannins, especially in late broods. Blue tits grow less well with tannin in their diet (Perrins, 1979).

(4) **Wound-induced chemical mechanisms**. Haukioja and Niemelä (1979) found that the larval period of Lepidoptera and Hymenoptera was protracted when larvae were reared on birch leaves adjacent to leaves which had earlier been mechanically damaged. Such an induced change in food quality, interpreted as defensive on the part of the birch, did not occur after leaves had attained their final size in late summer.

According to a hypothesis of Edwards and Wratten (1983, 1985), wound-induced responses of plants play an important role in determining patterns of insect feeding. Ecological evidence for damage-induced changes in leaves concerns the overdispersion of grazing damage at the end of the season: the pattern of damage beween leaves is often heavily biased towards a large proportion of leaves receiving a low level of grazing. Further evidence is the induction of unpalatability and chemical changes following damage by insect grazing. Edwards et al. (1986) assessed the palatability of damaged and undamaged leaves of 15 British tree species using larvae of the *Spodoptera littoralis* (Lepidoptera) in laboratory bioassays. Ten species exhibited significant wound-induced declines in palatability. Recently it has been suggested that attacked trees communicate with unattacked trees in the same vicinity to stimulate protective chemicals in these trees as well (Baldwin and Schultz, 1983; Rhoades, 1983). However, in studies with the western tent caterpillar (*Malacosoma californicum pluviale*) Myers and Williams (1984) found no evidence for induced anti-herbi-

vore defences in red alder (*Alnus rubra*). Results from Rhoades's study may be due to an infectious disease transmitted between caterpillars and not to intertree communication (Fowler and Lawton, 1985).

Fowler and Lawton (1985) have argued that most induced responses in damaged leaves may have negligible consequences for insect field populations. Tuomi et al. (1984) studied the system *Oporinia autumnata* — *Betula pubescens* ssp. *tortuosa* in Finland, and hypothesized that defoliation changes the carbon/nutrient balance in the plant, leading to a diversion of carbon to secondary metabolite production as a result of nutrient stress. Hence allelochemicals may be manifestations of this mechanism rather than active defensive responses by trees. There are even reports that moderate grazing by herbivorous insects may improve food quality (Williams and Myers, 1984). Fall webworm (*Hyphantria cunea*) larvae raised on foliage from red alder trees that had been attacked previously by populations of the western tent caterpillar grew faster and attained heavier pupal weights than did those raised on unattacked leaves.

(5) **Early leaf abscission**. Faeth et al. (1981) presented evidence that early leaf abscission is a cause of mortality for folivores. The authors studied three species of oak (*Quercus hemisphaerica*, *Q. nigra*, *Q. falcata*) and constructed life tables for two species of leaf miners, *Brachys ovatus* (Buprestidae) and the moth *Tischeria citrinipennella* (Tischeriidae). Per cent contribution to mortality of *B. ovatus* and *T. citrinipennella* respectively were: predation 15.8 and 16.7; parasitism 28.9 and 27.8; leaf fall 34.2 and 38.6; and other causes 21.1 and 16.7. Total mortality for the two species from egg through pupal stages was very high (95% and 90%). The leaf-mining larvae of the fly *Phytomyza ilicis* cause premature and unseasonal leaf fall in the holly, *Ilex aquifolium* (Owen, 1978). Perhaps the holly trees keep the proportion of mined leaves low by shedding them prematurely, while *P. ilicis* is still in the larval stage. However, in all these cases the effect of premature leaf fall on the trees and possible benefits have not been quantified.

(6) **Compensatory plant growth**. Partial defoliation can increase the efficiency of the remaining leaves (Harper, 1977) and may lead to a flush of new foliage which is photosynthetically very efficient (Kulman, 1971); however, this response requires additional nutrients (see Chapter 9).

Seed predation

Seeds are a highly valuable food resource for microbes, fungi, nematodes, insects, birds and mammals (Janzen, 1978). The availability of seeds is an important determinant of the population dynamics of seed predators. Populations of tits (*Parus* spp.) fluctuate in relation to seed crops because of changes in survival rates (Perrins, 1979). In response to a rich tree-seed supply, the granivorous voles *Apodemus sylvaticus* and *Clethrionomys glareolus* in southern Sweden lengthened the period of reproduction, had higher body weight and increased in population density during the same autumn, the next spring and occasionally even during the following autumn (Hansson, 1971). Outbreaks of the bank vole *C. glareolus* in a Danish deciduous forest only occurred in years following mast years of beech, *Fagus sylvatica*. Intensive winter reproduction preceded the outbreaks. The onset of the growing season is usually a stressful period for granivorous animals, because most of the seeds remaining in the resource pool germinate, and seeds become quite limited in availability until the new crop is produced in autumn. Hence many granivorous birds switch to feeding upon insects at the beginning of the growing season.

Seed mortality caused by granivores is often high (Golley et al., 1975; Crawley, 1983). In an English oak wood the probability that an acorn could produce a year-old seedling was less than 0.0006 (Shaw, 1968). In this forest small mammals were the principal acorn harvesters. Blue jays (*Cyanocitta cristata*) transported and cached 54% of the total mast crop from a stand of *Quercus palustris* trees in Virginia (U.S.A.); a further 20% of the crop was eaten by jays at the collecting site. A large number of the nuts remaining beneath the trees was parasitized by curculinoid larvae (Darley-Hill and Johnson, 1981). Estimates at Hubbard Brook (U.S.A.) suggest that mice consumed about 7% of the available seeds from the dominant tree species (Potter, 1978).

Mice also occasionally destroy a large number of tree seedlings (Hansson, 1971). However, it appears that seed predators have no long-lasting influence on the regeneration of woodland. Mice

may have an effect initially during reforestation, but exert no long-term effect on the structure of mature forests. The majority of studies suggest that most seedling mortality results from competition with existing trees (Harper, 1977).

There are three different types of defence mechanisms of trees against seed predation, all of which can be present in one tree population: chemical defence (Janzen, 1978); premature drop of infested seeds during summer; and the occurrence of mast years.

Seed predation seems generally to cause flower and fruit abortion (Stephenson, 1981) and the premature drop of infested seeds, responses which reduce wastage of energy on seeds unable to germinate. This phenomenon was demonstrated, for instance, by Boucher and Sork (1979): insect-infested fruits of the pignut hickory, *Carya glabra*, fell to the ground during summer, whereas viable fruits fell mostly during autumn. Infested nuts showed no growth after early August, aborted ones had increased in weight until late August. Viable fruits also had reached full weight in late August, but weighed significantly more than the other two categories.

The occurrence of mast years is a widespread phenomenon, usually interpreted as a mechanism for predator satiation (Janzen, 1971; Silvertown, 1980). Fruit and nut production of trees in temperate deciduous forests (such as beech [*Fagus* spp.]. oak [*Quercus* spp.], sugar maple [*Acer saccharum*]) varies dramatically from year to year (Richardson, 1977). In a Danish beech (*Fagus sylvatica*) forest rodents consumed 1.0 to 10.3% of beech seed production in mast years, and 30 to 100% between mast years (Jensen, 1982). Age structure of saplings revealed that most tree individuals had germinated in years following "mast" years, thus giving evidence for the predator-satiation hypothesis. During beech mast seeding in a Swedish deciduous forest, seed predation by vertebrates was lower than in a year with a moderate crop (Nilsson, 1985). However, the study suggests that mast seeding in trees is more effective in reducing seed predation by insects than by vertebrates. Beech reproduction tends to be synchronized by the weather over wide areas. During the evolution of masting behaviour those trees which tended to crop in the "wrong" years would have been less successful than those that were synchronized with most other trees. Different tree species tend to crop most heavily in the same years, and even those which have a crop annually (such as the birch *Betula pubescens*) tend to have much heavier crops in the years when the beeches have crops (Perrins, 1979).

Influence of animals on forest plant communities

Whittaker (1979) suggested that grazing may shift the competitive balance between grazed and ungrazed plants. Removal of green material often reduces root growth of shrubs and trees (Kulman, 1971). Dixon (1971) found that aphids (*Eucallipterus tiliae*) feeding on lime (*Tilia* × *vulgaris*) could prevent root growth. Modifications of shoot/root ratios and root activity, together sometimes with loss of below-ground material by rhizophages, may in turn affect the plant's ability to compete for light or nutrients.

Browsing may affect the competitive ability of tree species. Browsing by the white-tailed deer (*Odocoileus virginianus virginianus*) and other mammals has far-reaching effects on the species composition in eastern forests in the United States (Smith, 1976).

Herbivores can be vectors of tree pathogens — for instance, of the chestnut blight fungus *Endothia parasitica* causing the death of the American chestnut, *Castanea dentata* (Jaynes et al., 1976).

Mutualism

Is there a mutualistic relationship between herbivores and their host plants, namely forest trees, besides pollination and seed dispersal? Is even grazing or consumption of plant material by herbivorous animals directly advantageous?

Owen (1980) and Owen and Wiegert (1976, 1981) emphasized that grazing at levels below a certain threshold can benefit plants by recycling nutrients, fostering nitrogen fixation or other processes. Thus, many plants "need" grazers to increase fitness, but also need to keep the amount of grazing below harmful levels. A possible example is the premature leaf fall in the holly, *Ilex aquifolium*, caused by the fly *Phytomyza ilicis* (Owen, 1978). It is possible that by spreading out the season of leaf fall the fly is beneficial to the tree: year-round leaf fall may lead to a more even release of nutrients back to the tree than would occur if there were no leaf-miners present. How-

ever, hypotheses about mutualism between trees and herbivores are highly speculative and should be tested by relevant experiments.

Pollination

Flowering plants are a major constituent of deciduous forest ecosystems. For example, for adult Diptera in a Moravian lowland forest, visitation of flowers is the most important way of obtaining food (Vanhara, 1981).

Plants in the canopy, which is exposed, tend to be more often wind-pollinated; plants of the understorey and herb layer tend to be more often animal-pollinated (Regal, 1982). A "temperate trend" to anemophily exists in forests, although wind-pollination is usually not as effective as animal pollination. This trend may be caused by physical factors, clumping of trees, seasonality or historical factors (Regal, 1982). In an English oak forest wind-pollination is the usual method for the tree layer. Some species of the shrub layer are wind-pollinated, but in the field layer all species are insect-pollinated except dog's mercury, *Mercurialis perennis*. This species flowered exceptionally early (Neal, 1965). Proctor (1978), too, noted that woodlands (Querco-Fagetea) have the highest proportion of entomophilous herb species in comparison to other types of terrestrial plant communities in temperate latitudes.

An intriguing question is the role of competition between plant species for pollinators. An early view is that intense competition occurs for relatively few pollinators (Neal, 1965). According to this author, flowering times of insect-pollinated plants in English forests are considerably staggered, reducing competition for pollinators. Almost all plants, even those that are wind-pollinated, bloom before midsummer. Many plants appear in early spring. These adaptations can be explained by the wind-breaking effect of dense foliage, and by the fact that dense foliage conceals flowers from insects, decreasing the effectiveness of pollination (Neal, 1965). Of course the idea of resource partitioning between flowering plants along the niche dimension "seasonal flowering time" is an appealing concept. But it is not an established phenomenon. Phenological sequences may not be more than the outcome of random flowering times placed in order (Poole and Rathcke, 1979); competition may only be a weak force (Kevan and Baker, 1983). There are only a few experimental studies. In a mixed deciduous forest in Ohio (U.S.A.), Macior (1978) found no structural, behavioural or environmental characteristics of flowers or pollination, bumblebee queens being the base for a plant–pollinator association. In a mixed deciduous forest in Ohio (U.S.A.), there was no conclusive evidence that competition for pollinators was effective in excluding vernal plant species from the ecosystem (Macior, 1978). Except for possible interactions between the herbs *Dicentra* spp. and *Corydalis*, no clear evidence for competition between plant species for pollinators or between pollinators for forage has been observed. Motten (1986) found for a spring wildflower community of a deciduous forest in North Carolina that plant species are usually adequately pollinated. A characteristic set of floral biology traits securing adequate pollination is maintained within the community, including autogamy and self-compatibility, extended receptivity, and pollination by a variety of visitor types. Competitive effects between herbs, floral specialization or character displacement were not important.

Seed dispersal

Many plant species of temperate deciduous forests are dispersed by animals (Elton, 1966). Many canopy tree species are nut bearers, clearly adapted to animal dispersion. Additionally there are numerous herbs, shrubs and small trees with fleshy "fruits" (by this, I mean any soft covering around a seed that serves as an attractant and food source for a vertebrate dispersal agent; Thompson and Willson, 1978). Small seeds of herbs are often dispersed by arthropods such as ants.

In temperate deciduous forests, seed dispersal mechanisms tend to be related to the size of plant species (Harper et al., 1970). Herbs and low shrubs often bear hooked or hairy seeds that cling to the coats of passing mammals. Taller shrubs and small trees typically attract animals by offering fleshy "fruits". Large trees often produce large, heavy seeds. Opportunistic tree species tend to rely on light, numerous, wind-dispersed seeds. Most wind-dispersed plants are canopy trees or vines. Forest herbs often propagate by vegetative means

(Richardson, 1977). Where an animal is involved in seed dispersal, feeding habits, territoriality, and migratory behaviour may affect the distribution patterns of animal-dispersed plant species. The animal may eat and digest seeds (a loss to dispersal) or eat "fruits" and pass seeds undamaged in faeces (a possible gain to dispersal). Animals may transport seeds passively, or they may collect and bury seeds, giving rise to dense clumps of tree seedlings (Harper, 1977). The agents of dispersal may be specialized. Jays (*Cyanocitta cristata*) appear to choose species of the Fagaceae with small- to medium-sized nuts (*Quercus palustris*, *Q. phellos*, *Q. velutina*, *Fagus grandifolia*) and avoid the larger nuts of *Q. borealis* and *Q. alba* (Darley-Hill and Johnson, 1981).

The proportion of tree species dispersed by vertebrates is high in temperate deciduous forests (Howe and Smallwood, 1982), although many plants such as oaks (*Quercus*) and hickories (*Carya*) have nuts which are regularly hoarded by birds and mammals, and which lack clear modification for dispersal by animals (Smith, 1975). In an English oak forest studied by Neal (1965), most of the shrubs had edible "fruits" which were dispersed by birds. However, dispersal occurred mainly from outside to the interior of the wood, since only the shrubs at the edges of the wood and the borders of rides produced fruits. In the field layer the majority of plants had no specialized means of dispersal of fruits or seeds. In a mesic beech–maple forest in New York (U.S.A.), 67% of the 36 herbaceous angiosperms were animal-dispersed (Handel et al., 1981).

The distance that seeds travel may be short or long. In an English forest, tits (*Parus* spp.) usually removed and subsequently consumed fruits in the cover of nearby vegetation, the birds travelling an average distance of 18 m. Thrushes (*Turdus* spp.) travelled an average distance of 48 m from a feeding site (Sorensen, 1981). For jays (*Cyanocitta cristata*), mean distance between seed trees and caches was 1.1 km (range: 100 m–1.9 km) (Darley-Hill and Johnson, 1981). According to the "escape hypothesis" (reviewed by Howe and Smallwood, 1982), seed dispersal for a greater distance certainly is advantageous. Lemen (1981) found that seedlings of the Chinese elm *Ulmus parviflora* occurring directly under adult trees suffered rates of attack from the elm leaf beetle *Pyrrhalta* (=*Galerucella*) *luteola* 580 times higher than rates for seedlings not directly under adult elms. Shaw (1974) observed that the survival rate of oak (*Quercus robur*) seedlings was very low underneath the canopy of mature trees because of the high grazing pressure of lepidopteran larvae. However, most seeds of bird-dispersed species are deposited in shade near the parent tree. Each species has evolved ways to survive in shade for a limited number of years until eventually an opening in the forest occurs (Smith, 1975).

Some studies have examined the phenology of the plants and seed selection by consumers in forest communities. Smith and Follmer (1972) observed that oaks and hickories, which frequently occur together in climax forests, each have a season of the year in which their seeds are the more desirable food: hickory nuts in fall and spring, acorns in winter. Stiles (1980) studied the presentation and dispersal of bird-disseminated fruits of woody plants in the eastern deciduous forests of North America in relation to the available dispersal agents. Timing of fruit presentation and latitudinal patterns in fruit abundance are correlated with fall migration of frugivorous birds. Summer small-seeded and large-seeded fruits employ a mixed group of bird and mammal dispersers outside the migratory period, avoiding mammalian seed predation through either very small or very large seed size. Fall high-quality fruits are presented during fall bird migration; they are taken by birds in high numbers, but are subject to invasion by micro-organisms before being harvested by birds. Low-quality fruits are also presented during fall bird migration, but since they are in competition with high-quality fruits they achieve only low levels of dispersal at this time. They persist over the winter because invasion rates by micro-organisms are low. Dispersal of these species may increase sharply if other resources become scarce. Sorensen (1981) examined the phenology of fruit trees and avian consumption in an English forest. Ripe fruits were eaten by birds from late August to until early May. Most of the fruit was eaten by tits and thrushes. These two families differed in their consumption patterns. Tits took fruits of *Bryonia dioica* (white bryony), *Lonicera periclymenum* (honeysuckle), *Rubus* spp. (bramble), *Sambucus nigra* (elder), *Solanum dulcamara* (woody nightshade) and *Tamus communis* (black bryony) at the

beginning of the season only, whereas thrushes consumed fruits of bramble, elder, hawthorn (*Crataegus monogyna*), ivy (*Hedera helix*), rose (*Rosa canina*) and sloe (*Prunus spinosa*) mainly in the middle and the end of the season. There was no correlation between feeding preference and the abundance of the fruits or their nutritive value with respect to total nitrogen, total protein, total carbohydrates, total fats or energy content. Sorensen (1981) concluded that other factors, such as palatability or content of other nutrients, may be important in determining the feeding preference of different species of frugivorous birds. Natural selection might favour plants producing fruits that are highly attractive to species of birds which disperse seeds into favourable habitats, but are repellent to those which do not.

Saprophagy and microphytophagy

Detritus is defined as all particulate organic matter >0.45 µm particle diameter, together with associated bacteria, fungi and microfauna. Coarse particulate organic matter (CPOM) has a diameter of >1 mm, fine particulate organic matter (FPOM) of <1 mm. Dissolved organic matter (DOM) can be utilized by the microflora and some members of the microfauna (such as zooflagellates).

Often it is difficult to distinguish between truly saprophagous animals and those feeding on microfungi or bacteria (the microphytophages). Many soil and litter animals consume as "saprophytophages" a mixture of these types of food. The majority of soil animals are apparently obligately or facultatively microphytophagous (Dash and Cragg, 1972; Anderson, 1975b). Within the soil mesofauna, the fungivores may even dominate. In a *Liriodendron* forest in the United States, approximately 60% of the total biomass of the soil mesofauna consisted of fungivores (McBrayer and Reichle, 1971). In a German beech forest on limestone, a large proportion of the collembolan fauna belonged to species which were mainly mycetophagous (Wolters, 1985; see Table 6.5).

Many saprophagous and microphytophagous species depend much more on favourable environments than do phytophages. Many Collembola, for instance, feed only under moist conditions (Joosse, 1975; Joosse and Testerink, 1977). Further differences from herbivores are: (1) saprophages do not have such a distinct seasonality as herbivores; (2) saprophages are not so closely interrelated with food resources as herbivores (except for "grazers" on the microflora; (3) saprophages presumably are not as specialized as herbivores; (4) saprophages are dependent on external microflora.

Types of food

Truly saprophagous animals belong to various functional groups: mainly shredders (comminuting leaf litter material), many of which are trophic generalists, and fine-particle feeders (utilizing fine detritus particles) (Anderson and Sedell, 1979). The whole leaf in litter is not fed upon indiscriminately; for instance, snails scrape or rasp the softer tissue, leaving the vein intact. Main categories of saprophages are carrion feeders (necrophages), dung feeders (coprophages), and saprophages *sensu strictu*. Soil amoebae are the main bacterivorous group, which may also consume Actinomycetes and yeasts (Heal and Felton, 1970). Many oribatid mites and Collembola feed on microfungi (Wallwork, 1976).

Degree of specialization

According to Anderson and Healey (1972) and Anderson (1975b), the majority of soil animals have surprisingly similar feeding habits. There is in general less evidence for food differentiation than in other trophic levels. Herbivores, for example, show a far higher degree of food specialization. Most decomposers may have evolved generalist feeding strategies because food is both spatially and temporarily heterogeneous, and is also of low nutrient status (Hassall and Rushton, 1982). However, as more detailed studies become available, evidence of specialization among decomposers has increased. In this connexion it is important to distinguish between what soil and litter animals ingest, and what is actually assimilated as food (see Chapter 9).

Macrofauna. There are many studies on food preference of the litter-inhabiting macrofauna. Dunger (1958), for instance, found mean preference for leaf litter by Diplopoda, Isopoda, Pulmonata and Oligochaeta as follows. Overwintered litter was preferred to fresh litter, and among fresh litter of different species the order of decreasing preference was: lime (*Tilia cordata*); ash (*Fraxinus*

excelsior); hornbeam (*Carpinus betulus*); alder (*Alnus glutinosa*); elm (*Ulmus carpinifolia*); sycamore (*Acer pseudoplatanus*); maple (*Acer platanoides*); beech (*Fagus sylvatica*); oak (*Quercus robur*). In a German beech-wood on limestone, feeding preference tests demonstrated that herb litter was preferred to canopy litter, ash and maple to beech litter, overwintered beech litter to fresh beech litter (Table 6.4).

Some recent studies have attempted to uncover the factors responsible for the specific food requirements of the saprophagous macrofauna. A few examples follow.

Satchell and Lowe (1967) demonstrated for earthworms (Lumbricidae) an association between food preference and a number of factors, including content of nitrogen, soluble carbohydrates and phenolic substances. The results of laboratory experiments with *Lumbricus terrestris* by Cooke and Luxton (1980) indicate a preference for fungal paper discs (with soil fungi *Mucor hiemalis* and *Penicillium* sp.) over bacterial discs (with *Pseudomonas fluorescens*), and a preference for contaminated discs over the controls. The fungal discs had a higher nitrogen content than either the bacterial or the control discs. The results suggest that microbial contamination makes a potential food source attractive to worms, and that the attraction of fungal contamination is greater than that of bacteria. However, Nielsen (1962) concluded that earthworms do not possess a trehalose, and since trehalose is an important storage carbohydrate of many fungi, worms may not digest all the fungal components of their diet. Satchell's (1967) observation of an inverse correlation between the palatability of litter and its total polyhydric phenol content might better be expressed as a positive correlation between palatability and microbial development on the leaf (Cooke and Luxton, 1980). Why do earthworms find microbially modified substrates so palatable? Probably microbial contamination of dead plant material releases phagostimulants attractive to earthworms and probably this contamination makes available carbohydrate and nitrogen resources which the earthworms can more readily utilize. Presumably the alteration of the physical nature of the leaves in the litter during the process of weathering is not important. Satchell and Lowe (1967) showed that there was little correspondence between the mechanical nature of leaf litter and its palatability.

Millipedes and isopods prefer weathered litter to freshly fallen leaves and wood (Schneider and Tschakaroff-Schuster, 1978). These animals prefer *Fraxinus* sp. and *Acer* sp. to *Fagus* sp. or *Quercus* sp. (Edwards, 1974). Neuhauser and Hartenstein (1978) found no correlation between phenolic content or water-extractable content and feeding preference. The food preferred by isopods and diplopods had higher percentages of lignin and phenolics and lower percentages of carbohydrates. However, Hassall and Rushton (1984) stated that palatability of litter to isopods is negatively correlated with physical and quantitative chemical defences and with low nutritive value. Sakwa (1974) studied millipedes in a sycamore wood in England. Acceptance of different types of decomposing material was correlated with its nitrogen content, the carbohydrate content and the moisture content. The microbiota act to release available food substances and to decrease the polyphenol content. Sakwa suggests that the release of simple sugars from complexes and polyoses increases the palatability of litter leaves and also indicates the nutritive value of the food. The polyphenol and tannin content counterbalances the effect of sugars upon palatability.

In summary, studies on Isopoda, Diplopoda, Gastropoda and Lumbricidae have shown broadly similar patterns, in that litter of such tree species as alder, ash or elm is generally preferred to that of beech and oak; and that weathered litter is preferred to fresh litter. However, agreement has not yet been reached on the relative importance in food selection of physical factors such as hardness and hairiness, water content, taste substances such as tannins, and such chemical factors as the calcium content, protein content and C/N ratio (Satchell and Lowe, 1967).

Mesofauna. Many Collembola are fungal feeders (see, for instance, McBrayer and Reichle, 1971). They may be rather indiscriminate as consumers of fungi (Anderson and Healy, 1972; McMillan, 1975), although some recent data from laboratory preference tests have indicated selectivity by Collembola among different species of fungi and yeasts — for instance, by *Onychiurus armatus* (McMillan, 1975). According to Kilbertus and Vannier (1979), surface-dwelling Collembola of the

TABLE 6.4

Food preference of some species of the litter macrofauna in a beech-wood on limestone (Göttinger Wald)

Animal species	Temperature	Unit for consumption	Litter species (quality)[a]										
			Fa (f)	Fa (f) (su)	Fa (f) (sh)	Fa (o)	Fa (o) (su)	Fa (o) (sh)	Fr (f)	Ac (f)	Me (f)	Ga (f)	Ox (f)
Lumbricidae[b]	10°C	mg dry wt g^{-1} fresh wt day^{-1}											
Lumbricus terrestris						2.3[e]					5.0	3.9	11.5
						1.3[e]					20.9		
						3.3[e]						8.9	
						2.9[e]							23.9
											10.6	7.8	
											20.8		21.1
												6.6	21.5
						15.2[f,i]							
Gastropoda[c]	15°C	mg dry wt g^{-1} fresh wt day^{-1}											
Perforatella incarnata			0.2			0.2[g]			0.4	13.4	3.1	4.0	
Trichia hispida			0.2			0.2[g]			0.4	22.1	3.4	5.8	
Diplopoda[d,h]	10°C	mg dry wt g^{-} dry wt day^{-1}											
Glomeris marginata			0			46				88	26		
Glomeris conspersa			0			81				155	48		
Mycogona germanicum			0			144				87	35		

[a]Fa = *Fagus sylvatica*, Fr = *Fraxinus excelsior*, Ac = *Acer pseudoplatanus* and *platanoides*, Me = *Mercurialis perennis*, Ga = *Galium odoratum*, Ox = *Oxalis acetosella*, f = freshly fallen leaves, o = overwintered leaf litter, su = sun leaf, sh = shade leaf.

Based on mostly unpublished data from:

[b]K. Poser (Lumbricidae).

[c]Corsmann (1984 and pers. comm., 1986) (Gastropoda).

[d]T. Sprengel (Diplopoda).

[e]Collected 10 July 1980.

[f]Collected 2 October 1980.

[g]Collected in spring 1980.

[h]Collected 30 December 1980.

[i]Only this type of litter offered.

genera *Orchesella* and *Tomocerus* feed mainly on fungal mycelia; however, their food included spores, hyphae, plant membranes, parenchyma, tracheae, pollen, algae, organs such as bristles and scales, exuviae, crystals and amorphous elements. Wolters (1985) demonstrated the high diversity of food items in forest-inhabiting Collembola, and the seasonality in preferred food (Table 6.5). In field experiments, Collembola preferred soil fungi to bacteria. Most attractive was the fungus *Trichocladium opacum*. Differences in food selection are in some cases related to microhabitat differences. For example, in a coppice of sweet chestnut (*Castanea sativa*) *Tomocerus minor* and *T. longicornis*, which live in the more compact raw humus horizons with high fungal activity, took more fungal food than *Orchesella flavescens*, which is associated more with the layer of uncompacted leaf litter (Anderson and Healey, 1972).

Earlier authors suggested that many oribatid mites are unspecialized feeders, consuming leaf debris, fungal hyphae and spores and humic material (Hale, 1967; Bödvarsson, 1970; Anderson and Healey, 1972). However, oribatid mites appear to be far more specialized in the use of their food resources (Luxton, 1979; Usher et al., 1982); Wallwork (1983) calls them "principally fungivorous", although there are macrophytophagous species feeding on dead material of higher plants (Schuster, 1956). By using factorial analysis for the mesofauna of an oak wood, Cancela da Fonseca et al. (1979) showed that *Oppia nova*, other oribatid mites (such as *Nanhermannia elegantula*) and some other mesofaunal groups (such as *Folsomia penicula* [Collembola]) fed on cellulolytic fungi, in particular *Oidiodendron echinulatum*. Mitchell and Parkinson (1976) studied the feeding ecology of five mite taxa in a Canadian aspen (*Populus tremuloides*) wood. All taxa fed predominantly on pigmented fungi; the O_f and O_h inhabitants showing a higher proportion of hyaline fungi in their diet than the L (litter) inhabitants. Swift et al. (1979) emphasized that, in contrast to laboratory results, there was little evidence of selectivity in many field populations of mites or Collembola.

Grazing

Satchell (1974) and Parkinson (1983) have summarized the possible interactions between soil microflora and soil fauna: (1) transmission of microbial inoculum by animals, either on the body surface or by passage through the gut in a viable state; (2) increase, by comminution, in substrate surface exposed to microbial growth; (3) possible enhancement of microbial activity by changes in the chemical composition of organic material passing through the animal gut; (4) direct stimulatory or inhibitory effects by grazing on the microflora population. The phenomenon of "grazing" is frequently discussed, but there are few quantitative data on population dynamics of the biota.

Bacteria. Protozoa and bacteria apparently form an important predator–prey system in the soil of deciduous forests, particularly in the rhizosphere (Wallwork, 1976), though it is not yet clear how the bacterial populations are affected by their predators. Of course prey populations also act on the predators. Stimulation of amoebae by exudates of edible micro-organisms suggests that exudates can act as a "token stimulus" which indicates the presence of food and retards encystment (Heal and Felton, 1970). Microflora that are inedible or support litter reproduction tend to produce exudates that inhibit or do not affect activity.

According to studies of Kuserk (1980), cellular slime moulds (Dictyosteliida) are food-limited. In an oak–beech forest in Delaware (U.S.A.), *Dictyostelium mucoroides* responded to seasonal changes in bacterial biomass, spring and fall being peak seasons. The addition of various bacteria to field plots caused a significant increase in numbers of *D. mucoroides*. Moreover, the ability of this species to respond to a second addition of bacteria, made several days later, depended on the slime-mould density. High-density populations failed to respond to additional food, whereas those which had already returned to base levels, increased. Horn (1971) hypothesized that the quality and quantity of soil bacteria regulate the slime-mould populations and community composition.

However, even in laboratory microcosms the interrelationships are complicated. In a culture of *Tetrahymena pyriformis* with *Klebsiella*, *Rhizobium* or *Xanthomonas* as bacterial prey, predator and prey coexisted without typical oscillations. More prey survived as predator numbers were increased, possibly as a result of increasing toxicity of the medium and increased competition between preda-

TABLE 6.5

Food spectrum of different species of Collembola in a beech-wood on limestone (Göttinger Wald), based on analysis of gut contents. Numbers = mean value of 5 individuals, in parentheses standard deviation. Based on unpublished data of V. Wolters (pers. comm., 1986)

Species	Date	Type of gut contents						
		hyphae	spores	pollen	algae	plant material	amorphous	mineral
(A) Seasonal changes in gut contents (litter samples)								
Tomocerus flavescens	4 Dec 1979	2	34	0	0	4	41	19
		(1.8)	(31)			(4)	(12.5)	(13.5)
	5 Mar 1980	2	4	0	0	10	36	39
		(1.8)	(2.4)			(0)	(5.5)	(20.7)
	24 Jun 1980	10	19	1	0	13	42	14
		(7.1)	(7.5)	(2.2)		(4.5)	(13)	(5.5)
	22 Aug 1980	23	29	0	0	1.4	38	7.4
		(14)	(20)			(2.1)	(18.9)	(7.9)
	16 Sep 1980	26	45	1	0	3	15	10
		(13.8)	(12.3)	(2.2)		(2.5)	(4.1)	(0)
(B) Comparison of gut contents between different species (litter samples)								
Onychiurus "scotarius"	22 Aug 1980	1	33	0	0	4.2	48	13
		(0.5)	(17.2)			(1.8)	(13)	(4.5)
Onychiurus tricampatus	22 Aug 1980	2	52	0	0	2	37	6.1
		(4.5)	(16.5)			(1.9)	(15)	(3.2)
Folsomia quadrioculata	22 Aug 1980	0	51	0	0	3.4	41	6
			(19.5)			(4.2)	(17.5)	(2.2)
Tomocerus flavescens	22 Aug 1980	23	29	0	0	1.4	38	7.4
		(14)	(20)			(2.1)	(18.9)	(7.9)
(C) Gut contents of individuals on tree trunks (sampled with arboreal photo-eclectors)								
Tomocerus flavescens	19 Aug 1980	7.4	36	+	34	1	22	0
		(12.8)	(11.4)		(19.5)	(2.2)	(11)	
Orchesella flavescens	19 Aug 1980	4.2	35	1	21	5.2	28	2.4
		(5.3)	(30.8)	(0.5)	(25.1)	(8.5)	(13)	(4.3)

tors — that is, interference during grazing or cannibalism (Habte and Alexander, 1978).

Fungi. Grazing by the mesofauna can stimulate fungal growth and respiration. Satchell (1974) emphasized that there are both stimulatory and inhibitory effects on fungal populations, although exact quantitative data are lacking. Microphytophagous animals can cause distinct changes in the composition of the microflora (Anderson and Bignell, 1980). For example, grazing by the springtail *Onychiurus subtenuis* affected the competitive saprophytic ability of fungi colonizing fallen aspen (*P. tremuloides*) leaves in a Canadian forest (Parkinson et al., 1979). Two fungal species (a sterile dark form and a basidiomycete) were able to colonize aspen leaf discs in microcosm experiments. The sterile dark fungus was the most successful colonizer in the absence of Collembola, whereas the basidiomycete was the most successful colonizer when *O. subtenuis* was present.

Mitchell and Parkinson (1976) list possibly important interactions between oribatid mites and fungal populations. Mites may influence fungi by removing fungal hyphae or by disseminating propagules. Fungi may influence mites as a source of food or by toxin production. These processes affect population dynamics, community structure and decomposition rate. Pherson (1980) found evidence for the role of arthropods in the dispersal of microfungi (*Penicillium*, *Cladosporium*, *Trichoderma*) in beech (*Fagus grandifolia*) litter. (See the more detailed discussion in Chapter 9.)

Zoophagy

Apart from parasites, which are not considered here, important predatory and parasitoid groups in temperate deciduous forests are Chilopoda, Araneida, many mites, many Coleoptera and Hymenoptera (Blandin et al., 1980; Dajoz, 1980; Schaefer, 1983a, b). Many of the species inhabit the ground zone and the vegetation layer (such as ants or parasitoid Hymenoptera), but it is difficult to quantify how far these strata are interrelated.

Degree of specialization

As a rule there are many general feeders in the litter layer. Beetles, especially the Carabidae, have been well studied (for instance, Thiele, 1977; Dennison and Hodkinson, 1983a). An example of the diet of a polyphagous species, *Abax parallelepipedus* is given in Fig. 6.10. This carabid beetle is an opportunistic predator which shifts its diet in response to seasonal changes in prey abundance. Koehler (1984) demonstrated a similar polyphagy for *Pterostichus* spp. Loreau (1983) observed a tendency to specialization in medium-sized carabid beetles, which prey mainly on springtails. The scarcity of food in the litter may be the reason for the opportunistic behaviour of predators in this layer.

Formica rufa is a general feeder in the canopy layer. As an inhabitant of mixed woodlands on limestone in England, it preys upon abundant animal species, such as aphids (mainly *Drepanosiphum platanoides*), Diptera (mainly Bibionidae)

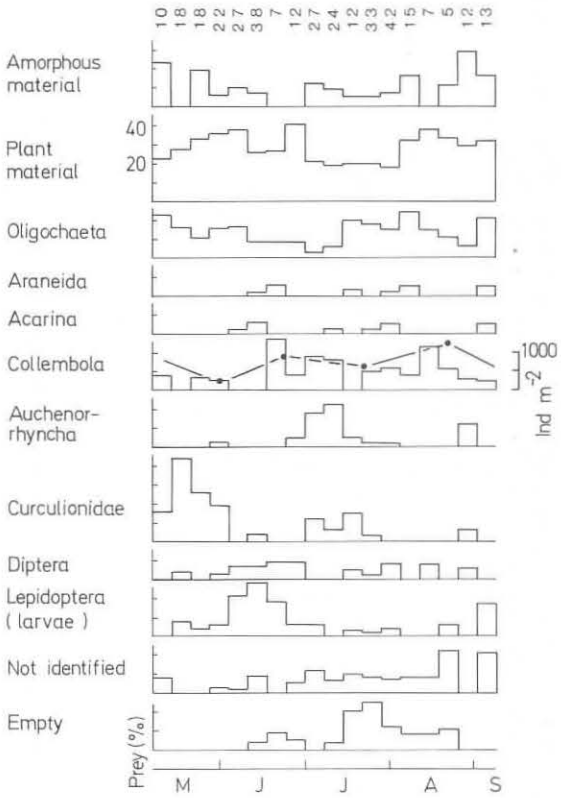


Fig. 6.10. Food spectrum of *Abax parallelepipedus* in a beech-wood on limestone (Göttinger Wald), based on analysis of gut contents. Numbers in the upper row: number of individuals studied. % = % of individuals with the indicated category of "prey" in the gut. For Collembola the number of individuals in the litter layer is given. Based on unpublished results of C. Martius (1986); data for epigeic Collembola from V. Wolters (pers. comm., 1986).

and Lepidoptera larvae (mainly *Operophthera brumata*) (Skinner, 1980). A high percentage of parasitoids, even, are polyphagous. In leaf-miner (*Phyllonorycter*) communities in English deciduous forests the mean ratio of polyphagous to specific parasitoids was about 6:1; in communities linked to *Quercus* galls the ratio was similar if the inquiline Synergini were excluded from the analysis (Askew, 1980).

Insectivorous birds have a high plasticity in foraging techniques and food choice during the non-growing season, because of the low numbers of active insects (Potter, 1978). A further example of a generalist is the shrew *Sorex araneus*. During a study in a scrub–grassland in England by Churchfield (1982), major prey items in all seasons were adult Coleoptera, insect larvae, Araneida, Opilionida and Isopoda. Approximately 40% of prey taken were less than or equal to 5 mm in body length, with only a few being smaller than 3 mm. This prey spectrum was correlated with the preponderance of small invertebrates, particular Staphylinidae, in the soil/vegetation cores. The diet of *S. araneus* showed no correlation with the relative activity of prey on the ground surface. Although there was little correlation between seasonal prey availability and the diet of the shrews, an increase in abundance of adult Coleoptera was accompanied by an increase in predation by shrews. Rudge (1968) found a close correlation between the abundance of secondary prey items and their contribution to the diet of *S. araneus*. Lumbricidae, Isopoda and snails, which are large prey items, were prominent in the diet of *S. araneus* in all months in this study, despite changes in their availability. However, the occurrence in the diet of secondary food groups such as Lithobiidae, Araneida and insect larvae was more closely correlated with their availability.

Interaction between predator and prey populations

Lawton and McNeill (1979) have stressed the importance of natural enemies in reducing the population sizes of phytophagous insects. However, experimental evidence is largely lacking. If predators are limited by their food resources, it does not follow that the predator is necessarily a limiting factor for the prey population (Schaefer, 1981). It should be borne in mind that in natural ecosystems the multispecies systems of predators and prey populations are difficult to analyse. Macropredators, for example, may remove parasitized larvae and thus negatively influence the population dynamics of the parasite.

There are some studies demonstrating the importance of predation pressure in the litter layer of deciduous forests (for instance, Clarke and Grant, 1968; Blandin et al., 1980; Dajoz, 1980; Schaefer, 1983b). Faeth and Simberloff (1981) performed an elegant study in the vegetation layer. Isolation of oak trees (*Quercus*) resulted in decreased parasitism and higher survivorship for larval leaf miners in comparison to larger stands of oak.

Ants and insectivorous birds have both been well studied. The importance of ants as predators in the canopy layer of deciduous forests is controversial. Skinner (1980) considered them to be potentially effective control agents of insect populations. The ant *Formica obscuripes* is attracted to extrafloral nectaries of the black cherry, *Prunus serotina*, and preys on many insects found on *P. serotina*, including the eastern tent caterpillar *Malacosoma americanum*, thus reducing defoliation by tent-caterpillar colonies (Tilman, 1978). Horstmann (1982) emphasized the importance of *Formica polyctena* in the energy budget of the consumer level in a forest. Populations of *Formica rufa* significantly reduce the abundance of lepidopteran larvae and aphids on sycamore (*Acer pseudoplatanus*), and thus contribute to lower levels of herbivory in the canopy (Warrington and Whittaker, 1985a, b; Whittaker and Warrington, 1985). Birds influence the population dynamics of many forest insects (Otvos, 1979). However, it can be doubted whether insectivorous birds normally play a significant role in controlling the abundance of their prey, although they may reduce the growth rate of the prey populations. Perrins (1979) regarded tits as not being important predators.

Key-factor analysis is an important method for uncovering the controlling influence of enemies on animal populations (Dempster, 1975). A famous example is the study of the winter moth, *Operophthera brumata*, in an English mixed woodland (Varley and Gradwell, 1968). Predation was significant for this population (Frank, 1967). Of 269 larvae per square metre falling to the ground to pupate, 238 were healthy. About 50 were killed by the pupal parasite *Cratichneumon culex*. Some 95

of the resultant 188 pupae were taken by adults of the carabid genera *Pterostichus* and *Abax*, and by adults of the staphylinid beetle *Philonthus decorus*, of which *P. decorus* took the largest proportion. Additional pupae were taken by elaterid larvae. The shrew *Sorex araneus* and other small mammals accounted for about 50 pupae. On emergence, the moths were again subject to the attack of surface-active predators. Losses from predation were density-dependent.

SPECIES DIVERSITY

High faunal diversity is a characteristic feature of temperate deciduous forests. This is true for the animal communities in the soil and litter layer (Anderson, 1975b; Wallwork, 1976), in the herb layer, and in the canopy (Elton, 1966). In European beech forests there live more than 6800 animal species: over 350 Protozoa, over 380 worms, 70 land snails and slugs, 560 arachnids and tardigrades, 26 isopods, 60 myriapods, 5210 insects and 109 land vertebrates (Frei, 1940) (see Chapter 14). However, the deciduous forests of Europe are poorer in species than those of North America and East Asia, because mountains prevented most species from escaping extinction by retreating to more southern regions during glaciations. The eastern Asiatic forests are the richest in species, because they remained free from ice during the Pleistocene. North American forests have an intermediate position, since animal and plant species could move southward parallel to the mountain chains (Tischler, 1984).

Diversity in the soil–litter subsystem

Communities of forest soils contain a large number of animal and microflora species (Swift, 1976; Ghilarov, 1977; Anderson, 1975b, 1977, 1978a; Holm and Jensen, 1980; Kjoller and Struwe, 1982). More than 1000 species of animals may inhabit one square metre of woodland (Anderson and Healey, 1972). Several hundred species of the microflora can occur in 1 g of soil (Anderson and Healey, 1972; Swift, 1976; Holm and Jensen, 1980). Paradoxically, many soil biota are not trophic specialists and apparently coexist while utilizing similar food resources (Anderson and Healey, 1972), a situation which Anderson (1975b) has termed the "enigma of soil animal species diversity". However, Usher et al. (1979) suggested that more detailed comparisons between the microarthropods of the soil–litter community and the arthropods of the above-ground community would probably indicate lower diversities of the decomposer communities and higher diversities of the "grazer" communities.

Habitat divers

Habitat heterogeneity of litter is determined by the amount, types, shapes and ages of litter leaves. Depth of litter is a decisive factor, along with variations in microclimate (moisture, temperature), number of microhabitats, and spatial arrangement of units (Stanton, 1979; Uetz, 1979; Stevenson and Dindal, 1982).

Studies in micromorphology of the soil (Babel, 1972, 1975) indicate that it is spatially complex. Anderson (1978a) used a micropoint transect technique on $100 \times 100 \times 60$ mm deep, gelatine-embedded sections of the soil and litter profile for measuring microhabitat diversity. This method involves placing a microscope eye-piece graticule (10 mm in 0.1 mm division) on the surface of a soil section and identifying the microhabitat located on each 0.5 mm division under the stereo-microscope. For that purpose 24 types of microhabitats in an English *Castanea* woodland soil were chosen to represent the structural features on which the mesofaunal species may partition the soil and litter habitats — leaf and wood fragments of different size, roots, types of faeces, cavities of different sizes, etc.

Macrofauna. Three macrofauna groups are analysed in more detail: earthworms (Lumbricidae), spiders (Araneida) and staphylinid beetles.

Earthworms. Usually only 6 to 8 species are present (range 2–14) (Phillipson et al., 1976). This low diversity, as compared to many other soil animal groups, possibly reflects the fact that earthworms are less specialized in their microhabitat and food requirements. Stratification of earthworm species in the soil is comparatively indistinct. On the other hand, Phillipson et al. (1976) found considerable ecological separation by space, time and food preference for the 10 species in an English woodland. It might be argued that there is no

chance for the establishment of more species in that habitat, since the species pool capable of colonizing forest soils is limited. A similar number of earthworm species occur in a German beech-wood on limestone (Judas et al., 1989).

Spiders. The number of spider species in the ground zone may approach 100. They inhabit a diverse array of structures, such as leaf litter, grass tussocks, herbaceous vegetation and woody litter. The relative abundance of the ground-living spiders in a German beech forest followed a log-normal distribution (G. Stippich, pers. comm., 1986), indicating the random influence of numerous environmental factors on spider species abundance (May, 1981).

Species richness, diversity and equitability were all correlated with litter depth and habitat space within a guild of wandering spiders studied by Uetz (1975). Increased microhabitat diversity tends to increase species richness of litter spiders, since a greater variety of structural microhabitats are available to them. In a North American deciduous forest, spider species richness was greater in litter consisting of curled leaves than in flat litter (Stevenson and Dindal, 1982). But spider families are affected differently. Within forest litter, abundance of Lycosidae was greatest in shallow litter made up of flat leaves, and decreased with increasingly deep litter, which contained more bent and curled leaves. Abundance of Clubionidae, Gnaphosidae and Thomisidae increased as litter became deeper and more complex (Uetz, 1976, 1979).

Staphylinid beetles. Schaefer (1983a) analysed the guild of staphylinid beetles in a German beech-wood. Most of the 85 species were associated with the leaf litter; however, some of them preferred specific microhabitats such as herbs, bark (see Tables 6.2 and 6.3), fruiting bodies of mushrooms, dead wood, or burrows of small mammals. The types of dominance–diversity curves are given in Fig. 6.11. They did not correspond to the broken-stick distribution (typical for more homogeneous guilds) or the log-normal distribution (caused more by random effects of many factors). The upper part of the curve approached the geometric series distribution (which is characteristic of extreme habitats: May, 1981), especially when the species were ranked according to their biomass. Diversity and evenness were lower when they were

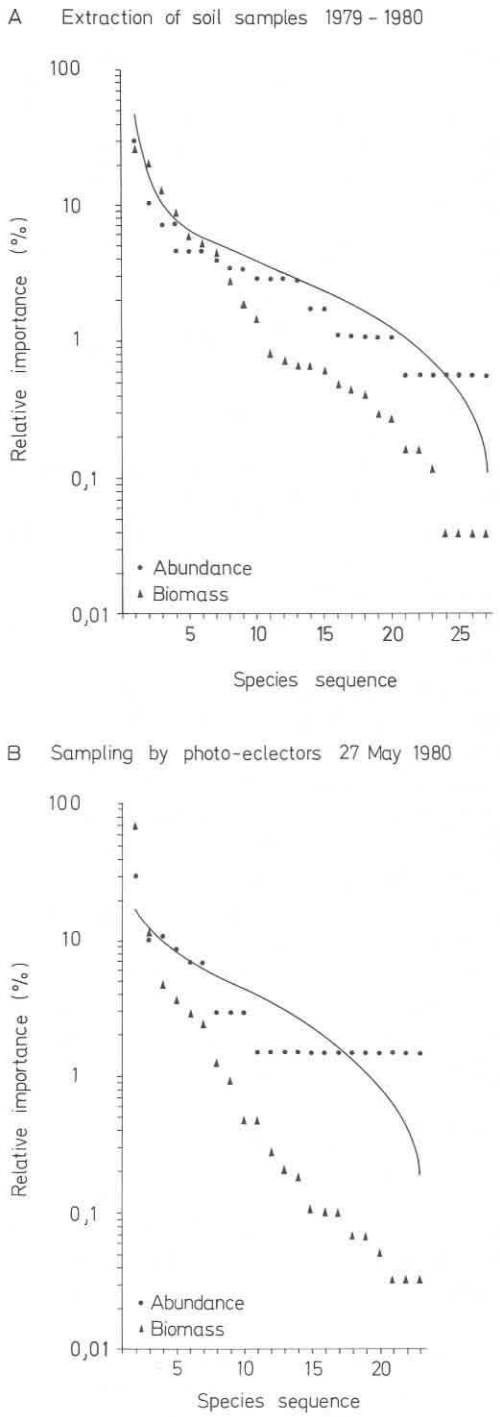


Fig. 6.11. Dominance–diversity curves for the staphylinid beetles in a beech-wood on limestone (Göttinger Wald) collected (A) by extracting soil–litter samples and (B) by sampling with photo-eclectors (emergence traps). The species are ranked by their relative proportion of abundance and of biomass. Solid line: broken-stick distribution. Modified from Schaefer (1983a).

calculated by using biomass values instead of number of individuals. Presumably the beech forest is an extreme habitat for the staphylinid fauna, with a rather thin layer of leaf litter populated in high abundance by only a few species of beetles. However, the biomass of the total predatory macroarthropod litter community in the forest was not correlated with litter depth (M. Schaefer, pers. observ.).

Mesofauna. Anderson (1977) pointed out that gradients of microclimate stability and microhabitat complexity occur over soil and litter profiles. The surface subhorizons are usually characterized by lower microhabitat complexity and microclimates, which tend to be unstable in comparison to deeper soil layers and follow temporal climatic variations. These microhabitats usually contain a few cosmopolitan species of the mesofauna which are physiologically tolerant and are represented by large numbers of individuals.

Important and diverse groups are oribatid mites (for instance, 66 species in a Danish beech-wood, up to 100 species in other forests; Luxton, 1982) and Collembola (around 50 species: Wolters, 1985). Abbott et al. (1980) found a log-normal distribution of the 72 oribatid species in a North American hardwood catchment.

According to Wallwork (1983), diversity of oribatids generally is high compared with other soil microarthropods, such as Mesostigmata, Prostigmata, Astigmata and Collembola, yet forest soil oribatids are reputed to show less feeding specificity (Anderson, 1975b) than above-ground insect herbivores.

How can one explain the high diversity of groups of the soil mesofauna? Litter animals show a temporal sequence in feeding patterns. Some litter-inhabiting mesofauna differ in the proportion of microbial and dead plant material ingested shortly after leaf fall, when these components are fairly discrete (Anderson, 1975a, b). However, as the litter becomes more comminuted and the biomass of fungal hyphae declines, most soil animals become generalist feeders. There are several explanations for the phenomenon of high species diversity of trophic generalists (Anderson and Healey, 1972; Anderson, 1975b, 1978a). The most likely is the correlation with microhabitat diversity. Soil animals maintain a high degree of microhabitat specialization, and potentially competitive species may be spatially separated. This hypothesis has been suggested by Anderson (1978a) by examining the relationships between Cryptostigmata species diversity and the diversity of soil and litter microhabitats in an English *Castanea* woodland. Cryptostigmata species diversity was correlated with microhabitat diversity (Fig. 6.12).

Species diversity gradients of oribatid mites along soil profiles tend to show dominance by one or two species in the surface litter (L) and at depth (O_h), and a more even distribution of species abundances in the fermentation layers (O_f) (which leads to higher diversity values; see Fig. 6.12). The O_f subhorizon is composed of fragmented plant material, faeces of soil animals etc. and is structurally more complex than the L or O_h layer.

This spatial arrangement of species diversity values of the mesofauna corresponds to phases in microarthropod succession during litter decomposition. Anderson (1975a) observed a microseral

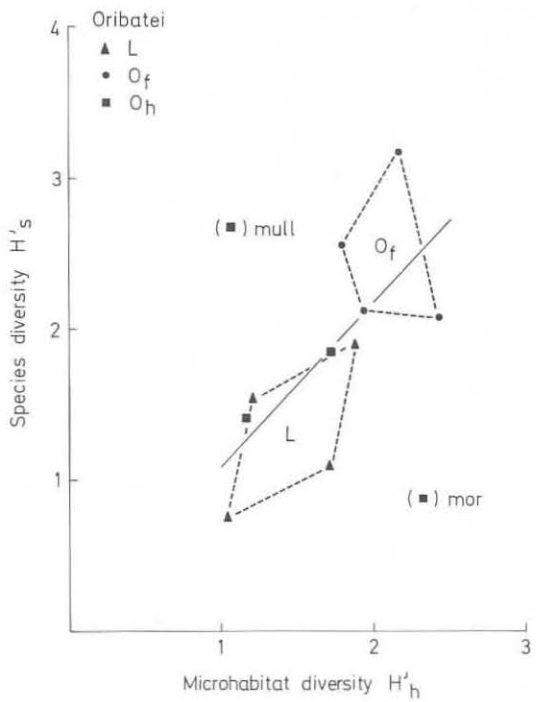


Fig. 6.12. Relation between species diversity of oribatid mites (Cryptostigmata) and microhabitat diversity in four woodland soils with mor, moder and "mull" humus forms. Regression line calculated without the 2 points in parentheses. Modified from Anderson and Hall (1977).

increase in diversity of Oribatei during the first year in decomposing chestnut and beech litter, promoted not only by the subdivision of food resources but also by an increase in microhabitat complexity. Species numbers and diversity then remained relatively constant during the following nine months. Hagvar and Kjøndal (1981) studied the succession of microarthropods (Collembola, Oribatei and Mesostigmata) in litter bags filled with decomposing birch leaves in a Norwegian spruce–pine forest for three years. Diversity rose during the first phase of succession and declined when "breakdown had reached a point where the number of available niches is reduced".

Diversity in the plant subsystem

In contrast to the soil–litter subsystem, animal populations of the herb or canopy layer in temperate deciduous forests are more closely linked to species composition, structure and architectural diversity of the plant community. Most studies concern herbivorous insects, which are analysed in more detail in the following paragraphs. There is no space to deal with other canopy arthropod groups. Phytophagous insects generally support a rich guild of their own parasitoids and predators (Lawton, 1978). Askew (1980) reported on the diversity of canopy parasitoids of leaf miners (*Phyllonorycter* spp.) and gall-forming Cynipidae. Southwood et al. (1982) noted on different tree species increasing diversity in the series epiphyte grazers, scavengers (dead wood and fungal feeders), phyllophages, "tourists" (non-predatory animal species which have no intimate or lasting association with the tree) and predators.

There are two aspects of species diversity in the vegetation subsystem: (1) the number of herbivore species associated with a particular plant species; (2) the number of above-ground animal species occurring in a given forest community. For example, Southwood et al. (1982) found 465 arthropod species on British oak trees, and 327 on British birch trees. Nielsen (1975) recorded about 250 free-living canopy insects in a Danish beech-wood. Crossley et al. (1973) found 272 coleopteran and hymenopteran species in a mixed hardwood coppice catchment (North Carolina, U.S.A.).

Habitat diversity

The herb layer may consist of numerous plant species (Hughes, 1975; Dierschke and Song, 1982). However, herb species richness in deciduous forests on mor or moder soils is low in most cases (Ellenberg et al., 1986). The canopy layer is characterized by a high structural complexity. Southwood (1978b) demonstrated the large surface area associated with an old beech tree (Table 6.6), which makes possible a remarkable habitat diversity. Morris (1974) described the structural diversity of oak trees, with roots, trunk and larger branches, twigs, buds, catkins, acorns, leaves, macrofungi, dead wood, rot-holes, nests — all allowing the existence of several thousand insect species.

Herbivores of the herb layer

Lawton (1978) demonstrated a general trend of increasing diversity of phytophagous insects from herbs through trees, but there are exceptions to this rule. A group that reverses the trend are the Agromyzidae (Diptera), which are scarce on trees and achieve their highest numbers on herbaceous plants (Askew, 1980); parasitoid communities of this dipteran family follow a similar trend.

In a German beech forest a total of 7 dominant curculionid and all chrysomelid beetle species were associated with the herb layer, as larvae and as adults; 7 curculionid and no chrysomelid species were inhabitants of the canopy layer, at least as adults (B. Wagner, pers. comm., 1986). In contrast, almost all of the 53 lepidopteran species fed during

TABLE 6.6

Habitat areas associated with an old beech (*Fagus sylvatica*) tree, without epiphytes. Modified from Southwood (1978)[b]

	Area (m^2)	
	in summer	in winter
Ground area covered by canopy	200	200
Living part of beech tree		
Surface of trunk	52	52
Surface of branches and twigs	230	230
Both surfaces of leaves	10 200	
Dead parts of beech tree		
Outer surface of branches	80	80
Inner surface of bark of branches	60	60
	c. 11 000	*c.* 650

their larval phase in the canopy layer (Winter, 1985).

Higher species diversity in the canopy layer than in the herb layer can be at least partly attributed to the complex architecture of trees.

Canopy herbivores

The number of phytophagous canopy arthropods varies between tree species. Ash (*Fraxinus excelsior*), for instance, supports relatively few phytophagous invertebrates: 41 species in Britain (Southwood, 1961). Oaks (*Quercus* spp.), on the other hand, have one of the richest insect faunas of any tree (284 species in Britain: Morris, 1974; Southwood et al., 1982). There are several hypotheses, not mutually exclusive, that try to explain such differences in faunal diversity.

(1) **Tree history**. According to a hypothesis of Southwood (1961), dominant native trees will have the most insect species, and recently introduced ones the fewest. The number of species of the major plant-feeding orders of insects (Lepidoptera, Coleoptera and most groups of Hemiptera) associated with British trees is closely correlated with the records of their Quaternary remains (Fig. 6.13A). When the effect of history is eliminated, some trees appear to be preferred (hawthorn, *Crataegus* spp.; willow, *Salix* spp.; sloe, *Prunus spinosa*; poplar, *Populus* spp.). Others appear not to have been as favourable for insect colonization (hazel, *Corylus avellana*; ash, *Fraxinus excelsior*). However, the length of time a tree species has been present in Britain is not a main determinant of insect species richness (Birks, 1980; Crawley, 1983; Strong et al., 1984).

(2) **Geographical range and tree abundance**. According to several authors (Southwood, 1961; Opler, 1974; Strong and Levin, 1979; Southwood et al., 1982; Strong et al., 1984) plants with large geographical ranges support more species of insects than rare plants (Fig. 6.13B). The former tree species are more likely to be found and colonized, given sufficient time. However, the influence of plant chemistry has to be considered (Lawton, 1978). The same relationship has been found for parasitic fungi on British trees (Strong and Levin, 1975). Southwood and Kennedy (1983) critically remarked that island biogeography theory is inadequate as an explanation of insect species richness on trees. In this connexion it should be emphasized that abundance (population density) is not synonymous with geographical range (Neuvonen and Niemelä, 1983), as is incorrectly assumed by many authors.

(3) **Plant architecture**. Relevant aspects of architecture (Lawton, 1983) are: size; growth form; seasonal development (that is, seasonal changes in size and growth forms); variety of above-ground parts ("modules", Harper, 1977); persistence of individual components (that is, longevity of modules). How might plant architecture influence insect diversity? Currently there are two principal hypotheses.

The first is the "size *per se*" hypothesis (Lawton, 1983). Large plants are more likely to be found and colonized by insects than are small plants, both in ecological and evolutionary time. Moreover, if large plants support larger total populations of insects, species losses through extinctions may be reduced. However, Southwood et al. (1982) found no clear relationship between the size of individual trees and the number of arthropod species found on them. Larger species of Finnish trees have richer macrolepidopteran faunas than smaller species of trees and shrubs (Neuvonen and Niemelä, 1981). On average, more species of Microlepidoptera attack individual species of British trees than single shrub species, and both have more species than herbs (Price, 1977). Preliminary studies on cynipid gall wasps of several North American oaks (*Quercus* spp.) suggest that architecturally simple stages (seedlings) support fewer species of insects than saplings, and they in turn fewer than mature trees (Lawton, 1983).

The second is the resource diversity hypothesis (Strong and Levin, 1979; Lawton, 1983). Plants with a greater variety of resource types (such as feeding, resting, overwintering and hiding places) support more species of herbivores than plants with fewer resources. There is much evidence for the diversification of basic feeding sites, occurrence of enemy-free space, vertical zonation of herbivores, changes in the herbivore community during season, and somatic mutations in trees (Whitham, 1978). Larger plants permit more possibilities both for avoidance of competition and avoidance of predators and parasites from neighbours (Lawton, 1978).

(4) **Taxonomic relatedness**. Comparing the species richness of different tree species, their taxo-

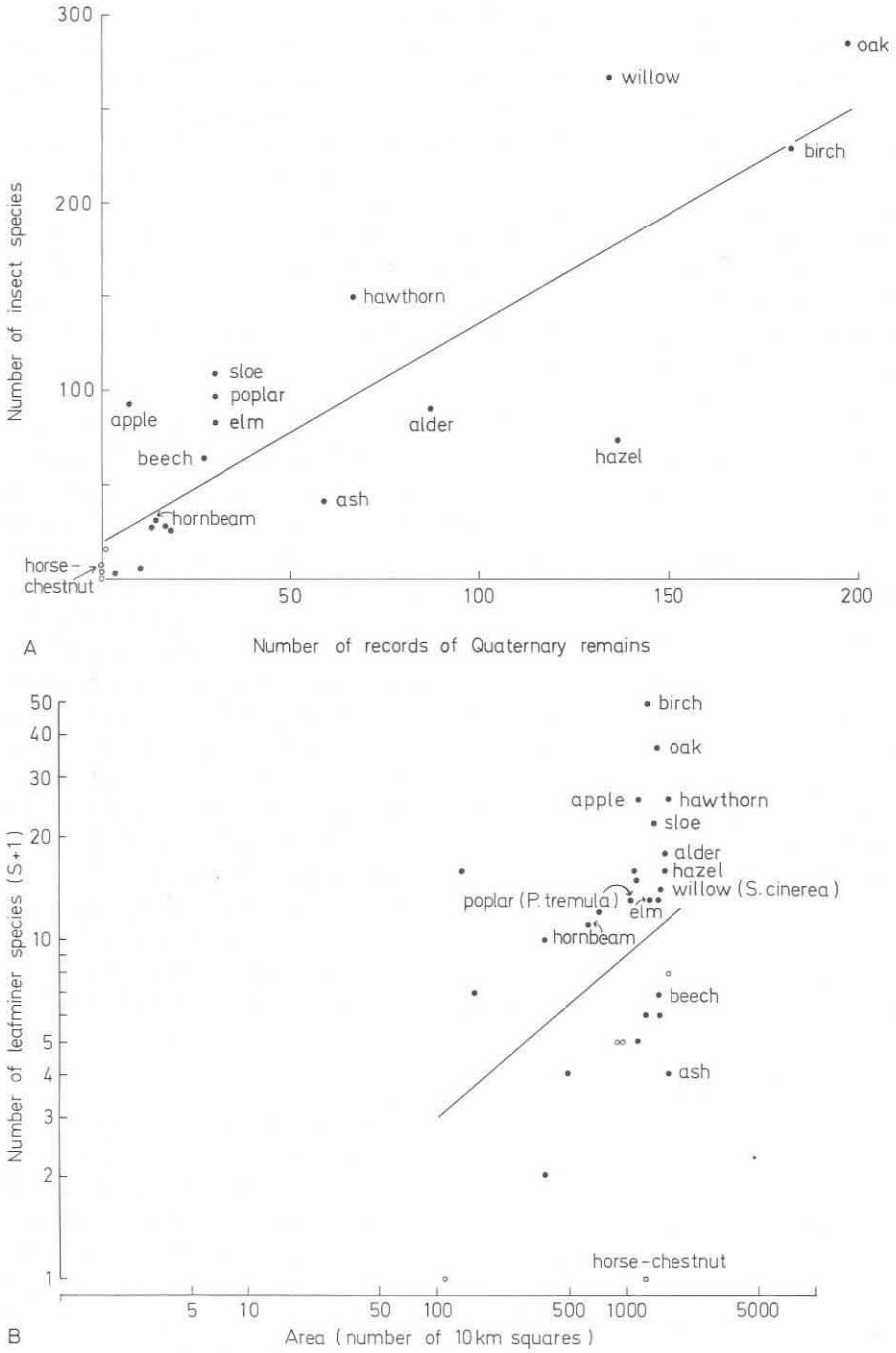


Fig. 6.13. Relationship between (A) the history of a deciduous tree species and the number of associated insects (data for British tree species after Southwood, 1961), (B) the area of a deciduous tree species and the number of associated leaf miners (for British tree species, modified after Claridge and Wilson, 1982).

nomic relationship and degree of isolation may be important in understanding chemical defence mechanisms ("biochemical distinctness") of the plants (Lawton and Schroeder, 1977), but also the feeding adaptations of the herbivore guilds. Neuvonen and Niemelä (1983), for instance, found that host plant frequency, the number of plant species per order, and the number of relatives of the host-

plant genus explained a total of 62 to 85% of the variation in species richness of Finnish trees and shrubs. This points to the importance of relatedness as a factor which determines the species richness of herbivores (Neuvonen and Niemelä, 1981). Architectural effects may be more difficult to detect within closely related, and hence more uniform, groups of plants. Small species of North America oaks are not noticeably more impoverished in their cynipid gall–wasp fauna than larger species (Cornell and Washburn, 1979).

In summary, it appears that the range of host plant species is a major predictor of species richness, rather than the size of the individual host tree. On present evidence, the range explains approximately 2.5 times as much of the variation in insect species richness on British plants as architecture (Strong and Levin, 1979). The variables log tree abundance, time present in Britain, whether or not trees were evergreen, taxonomic relatedness, tree height and leaf length contributed significant F values and accounted for 82% of the variation in insect species richness between British trees (Kennedy and Southwood, 1984). In this analysis the species/area relationship explains 58% of the variation. Generally the considerable amount of unexplained variation in total insect species richness may be the result of random patterns of host tree colonization.

Case study: leafhoppers and leaf miners

No clear general correlation between the history of the tree species and leafhopper species richness exists for the mesophyll-feeding Typhlocybinae, with a total of 62 species in Great Britain (Southwood, 1961). Some of the most recently occurring trees in the British flora, such as hornbeam (*Carpinus betulus*) and sycamore (*Acer pseudoplatanus*), have a much more diverse leafhopper fauna than would be predicted. Ash (*Fraxinus excelsior*) is attacked by only one leafhopper, *Empoasca vitis*, the most polyphagous species known (Claridge and Wilson, 1976). Claridge and Wilson (1981) calculated species/area relationships for 34 different tree and shrub species and their associated leafhopper species. The regression was significant, but explained only 16% of the variation. Thus host-plant range is also relatively unimportant in determining species richness of Typhlocybinae on trees. For broadleaved woodlands in South Wales, there was no clear-cut correlation between the proportional abundance of a tree species in the canopy and the number of associated typhlocybine leafhopper species (Claridge and Wilson, 1976). But it appeared that the fauna associated with each tree was very distinct and not taxonomically related. Obviously the diversity of the canopy leafhopper fauna (comprising many monophagous species) is more closely linked to the species diversity of the plants forming the habitat than to some measures of architectural diversity.

Claridge and Wilson (1982) also studied the species richness of leaf miners associated with 37 deciduous and coniferous trees and large shrubs in Britain (cf. Fig. 6.13B, which contains only the relationship for deciduous species). A significant relationship exists between range size of the host plant and the species diversity of associated leafmining insects, but the correlation explained only 19% of the variation about the regression line. A further 23% of the variation may be accounted for by taxonomic relationships of host plants. There was a significant correlation between leaf miners and mesophyll-feeding leafhoppers. Both guilds were dominated by host-specific feeders. The species/area effect is important in determining species of phytophagous insects mainly when groups of closely related host plants are considered. With more diverse arrays of hosts, taxonomic influences, which are probably mainly chemical, may outweigh such area-related effects (Claridge and Wilson, 1982).

Diversity during the season

According to the plant-architecture hypothesis, trees and woody bushes — with most of their structure already in place in spring — might be expected to fill up rapidly with species as soon as their leaves open. Such a relation was found for Lepidoptera on oak trees (Feeny, 1970; Lawton, 1978) (Fig. 6.14B). However, this pattern is modified by the influence of quantitative defences like tannins. As tannin levels increase and protein levels fall with season, the diversity of the lepidopteran fauna decreases. A similar but more delayed increase of species number was observed for the curculionid fauna of a German beech-wood (Fig. 6.14A). Nielsen (1974) noted a distinct peak of foliage arthropod activity in May in a Danish

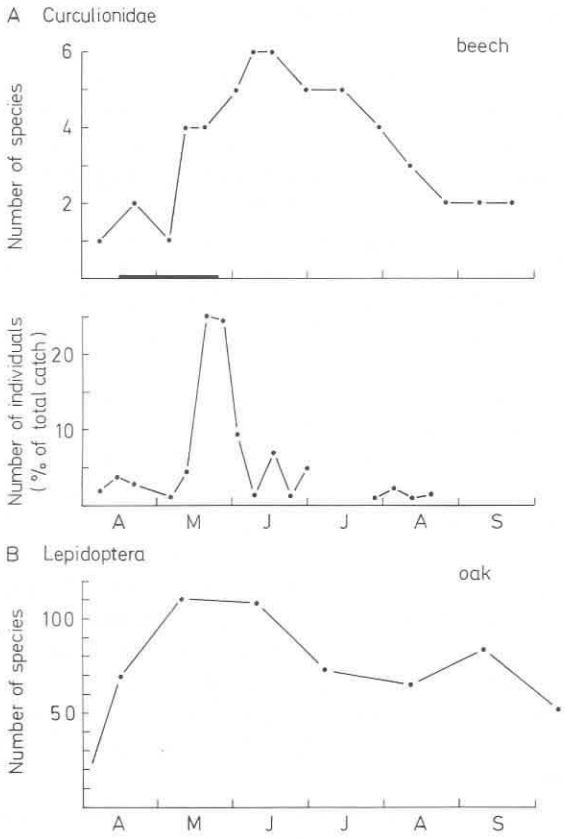


Fig. 6.14. Seasonal build-up of herbivorous insects in the tree canopy. (A) Curculionidae of a beech-wood on limestone (Göttinger Wald). Bar: appearance of the canopy leaves. Number of adult individuals as % of total annual catch with ground photo-eclectors (emergence traps) (based on unpublished data from Wagner). (B) Foliage-feeding Lepidoptera on oak (modified after Feeney, 1970).

beech forest, mainly due to the abundance of the predominant phytophagous insects, such as *Rhynchaenus fagi*, *Phyllobius argentatus* and *Operophthera fagata*. The majority of gall insects and leaf miners are present in May, too (Nielsen, 1978).

Finnish studies on tree-feeding Macrolepidoptera reveal seasonal patterns in diversity that are determined by the duration of the shoot-growth periods (Niemelä and Haukioja, 1982). Species that complete their shoot growth early ("*Quercus*" type) have new leaves present only in spring; macrolepidopteran diversity peaks early (that is, is positively skewed) on these species. Trees in which shoot growth continues to autumn ("*Populus*" type) have new growth present all summer and negatively skewed herbivore diversities (with a peak in autumn). A highly significant correlation ($r^2 = 0.96$) exists between the duration of the shoot-growth period of seven species of Finnish trees and the skewness for species richness of Macrolepidoptera over the season (Niemelä and Haukioja, 1982).

Habitat islands and species richness

The island-biogeography theory (MacArthur and Wilson, 1967) has been applied to single trees (discussion in Southwood and Kennedy, 1983), to host plants (Janzen, 1968, 1973), and to forest islands (for instance, Faeth and Kane, 1978; see discussion in Gilbert, 1980). This has been criticized for each of the above-mentioned cases: single trees (Southwood and Kennedy, 1983), host plants (Kuris et al., 1980), and forest islands (Connor and McCoy, 1979; Schaefer and Kock, 1979), mainly on the grounds that there is no equilibrium of immigration and extinction on the vegetation patches as required by theory.

According to Connor et al. (1983), the distribution and abundance of leaf miners on oak should not be viewed as the turnover of reproductive populations, but rather as the immigration and failed colonization of species whose movements encompass several trees. Faeth and Simberloff (1981) observed that leaf-miner populations, at least on small isolated oak trees, are maintained by continued re-immigration. Little or no *in situ* reproduction and colonization occurred on small isolated trees.

The fact remains that the number of animal species in a deciduous forest may be correlated positively with its size, if the forest is an "island". According to Shreeve and Mason (1980) there are two alternative hypotheses (besides the island equilibrium model) to account for the increase of species richness with area: Williams' (1964) habitat heterogeneity hypothesis (Strong et al., 1984), and the suggestion by Connor and McCoy (1979) that species number is controlled by passive sampling of a species pool, with larger areas receiving larger samples and hence more species than smaller areas.

In the following enumeration of examples it should be borne in mind that islands for larger vertebrate species are essentially "continents"

for the much smaller invertebrates (Kendeigh, 1979).

The maintenance of diverse forest bird communities requires large wooded tracts (Whitcomb et al., 1981). Both island size and the matrix in which the island is embedded influence the presence and abundance of certain mammalian species (Matthiae and Stearns, 1981). The number of small mammal species on Iowa (U.S.A.) woodlot islands was positively related to their size. Islands contained significantly lower densities of *Peromyscus leucopus* than "mainlands", and the density of *P. leucopus* was inversely related to isolation (Gottfried, 1979). The study supported several predictions of the MacArthur and Wilson model.

The number of butterfly species in 22 woods in eastern England was significantly correlated with the area of the woodlot, but not with the area of glades and rides, which provided both larval food plants and adult foraging sites (Shreeve and Mason, 1980). The number of vagile species, but not the number of poorly vagile species, was correlated with the area of woodland within 1 km of the studied wood, this being a measure of the sources of potential colonizers. It was predicted that a woodland area of about 460 ha would be required to support all the 26 species recorded in the study. The value of $z = 0.50$ was high;[1] high values of z have been attributed to highly interactive communities (Opler, 1974), and to non-equilibrium land-bridge systems. A maximum of 50% of the variation could be explained by variation in the woodland area.

Faeth and Simberloff (1981) tested population characteristics of a guild of leaf-mining insects on oak host plants (*Quercus falcata*, *Q. nigra*, *Q. hemisphaerica*) which had been experimentally isolated by transplanting them into an agricultural field. When all oak species were considered together, the isolated trees were colonized by slightly fewer species (12) than non-isolated trees (13). Species composition, however, differed between field and edge trees. There was no statistical difference between densities of leaf miners on field and edge trees.

[1] $x = a + zy$, where x is log (area) and y is log (number of species).

RESOURCE PARTITIONING

Partitioning of resources is postulated to be a basic mechanism permitting the coexistence of species within guilds. Are the guilds of animal groups in temperate deciduous forests organized in such a way that interspecific competition for essential resources is important? In a review, Schaefer (1980) came to the conclusion that interspecific competition in many cases is not a component of ecological separation in arthropods. A recent discussion by Simberloff (1982) suggested that competitive exclusion of one species by another one is exceptional and that, more frequently, species sharing resources either do not affect one another, or coexist with changes less drastic than local extinction. When species do compete with one another, effects are usually moderated by other factors (such as weather, predators, parasites) which keep populations below levels at which exclusion would occur, or else each competitor is favoured in a different set of times and/or places and this fact, combined with normal individual movements, keeps all species in the system.

In the following paragraphs some illustrative examples are presented concerning important phytophagous, saprophagous and zoophagous taxa.

Phytophages

Are herbivores food-limited? One answer is that they are not limited by their food supply, but rather by natural enemies which prevent their populations from increasing to densities at which competition for food may occur (Hairston et al., 1960; Crawley, 1983; Strong et al., 1984). A second answer holds that not all that is green is palatable and that food supply for herbivores might be limited (Whittaker and Feeny, 1971). The different quality of plant food material may thus be a limiting factor for certain herbivore population.

Canopy phyllophages

How are tree leaves utilized by leaf-feeding arthropods? Probably food shortages are rarely experienced by phyllophages, as total herbivory is low in many forests (see Chapter 9). However, several species may be potential competitors

because in the lower part of the canopy the grazing pressure can be comparatively high, and several species often attack the same leaf (Nielsen, 1978). Lawton and Strong (1981) and Strong et al. (1984) have doubted a significant influence of actual interspecific competition and even the "ghost of competition past" (Connell, 1980) is difficult to test rigorously.

Nielsen (1978) studied the position and zonation of miners and galls along beech leaves in a Danish beech forest. Nine of the ten dominant arthropod species demonstrated significant preferences for certain leaf zones (Fig. 6.15A, B). High frequencies of leaf miners and galls were recorded from the middle and basal leaf sections. Apparently the leaf apex is an unimportant microhabitat for stationary beech phyllophages, except for *Aceria stenaspis stenaspis* (Eriophyidae) and final leaf-mining stages of the beech weevil *Rhynchaenus fagi*. In old beech stands, feeding activity is largely concentrated in the lower canopy. Differences in feeding technique and position of feeding tracks of beech phyllophages on the leaf may contribute to food resource partitioning in the canopy layer (Nielsen and Ejlersen, 1977; Nielsen, 1978). Phenological differentiation may contribute to further subdivision of food resources in two cecidomyiid species, *Mikiola fagi* and *Hartigiola annulipes*.

Methodological difficulties have prevented detailed studies of ectophagous phyllophages. Investigations on mesophyll-feeding leafhoppers of the subfamily Typhlocybinae are an exception. More than 30 typhlocybine species can coexist in the same woodland (Claridge and Wilson, 1976). There are many striking examples of plants which support closely related leafhopper species in British woodlands: 4 species of *Edwardsiana* on alder (*Alnus glutinosa*), 4 species of *Eurhadina* on oak

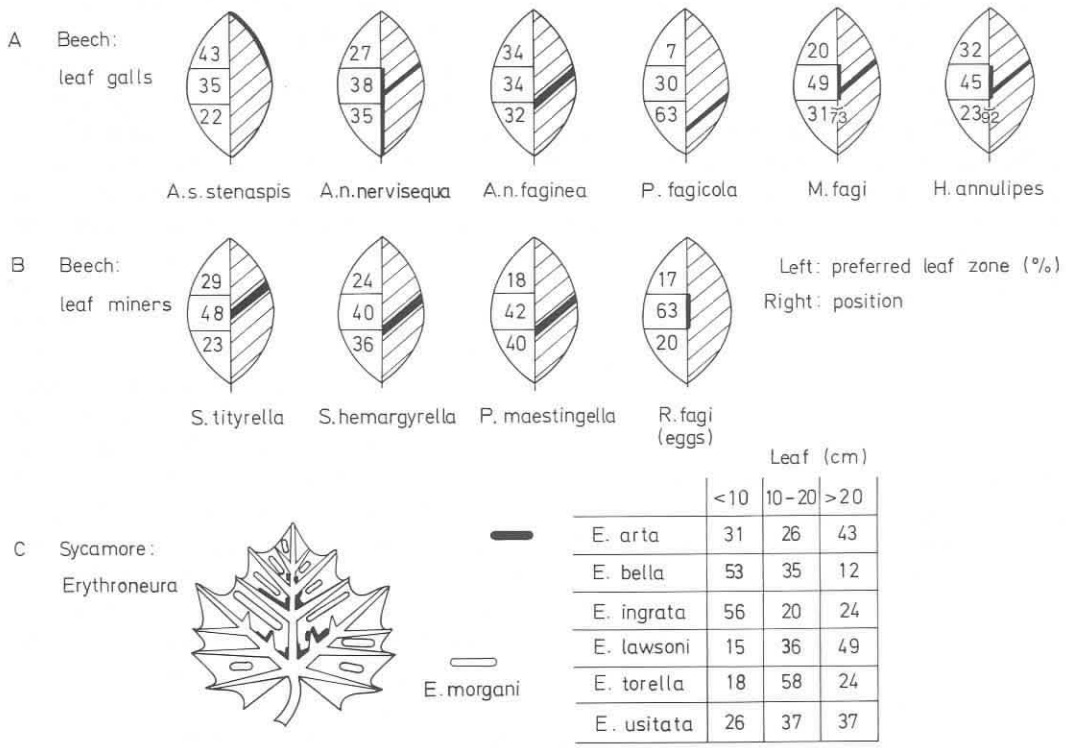


Fig. 6.15. Resource partitioning in canopy phyllophages. (A) and (B) Position and zonation of galls and miners on beech leaves in a Danish forest. For *Mikiola fagi* and *Hartigiola annulipes* percentage of galls near the midrib is indicated. Species: the eriophyids *Aceria stenaspis*, *A. nervisequa nervisequa*, *A. nervisequa faginea*, the cecidomyiids *Phegomyia fagicola*, *Mikiola fagi*, *Hartigiola annulipes*, the nepticulids *Stigmella tityrella*, *S. hemargyrella*, the gracillariid *Phyllonorycter maestingella*, the curculionid *Rhynchaenus fagi*. Modified from Nielsen (1978). (C) Occurrence of *Erythroneura* species (Typhlocybinae) on the lower surface of sycamore leaves, and on leaves of different width. Open symbols: distribution of *E. morgani* on the leaf; closed symbols: distribution of another species, for which preference of leaf width is given. Numbers are % of individuals. Modified from McClure and Price (1976).

(*Quercus robur*). There is little obvious sign of temporal separation which might reduce the effects of interspecific competition. Ross (1957) has described an apparently similar situation in North America, in which 8 species of *Erythroneura* co-occur on eastern sycamore, *Platanus occidentalis*. The most thorough analysis of coexistence of a guild of mesophyll feeders was made by McClure and Price (1975, 1976). These authors conducted rearing experiments in the field, with single species and mixed species, demonstrating competition between sympatric *Erythroneura* species on sycamore leaves. The relative rates of dispersal and local extinction among competing species may explain coexistence in the sycamore leaf-feeding guild (McClure and Price, 1975). McClure and Price (1976) examined five niche dimensions in detail (temporal utilization, distribution within the canopy, occurrence on leaves of various sizes and ages, location of feeding sites on the leaf) and studied three habitat or intercommunity parameters (occurrence on trees along a moisture gradient, latitudinal distribution with respect to that of sycamore, and distribution within a given geographic locality). There were insufficient differences between species in all five intrahabitat niche parameters to explain coexistence in the guild by niche segregation (Fig. 6.15C), except for *Erythroneura morgani* which had distinctly different feeding sites on the leaf. However, the two last interhabitat parameters could explain coexistence by habitat segregation.

Small mammals

In reviews, Grant (1972) and Chew (1978) showed that competition for space is probably a general phenomenon among rodents. Some recent studies have tried to demonstrate competition between rodent species in temperate deciduous forests.

The two rodent species *Apodemus sylvaticus* and *Clethrionomys glareolus* are sympatric in English deciduous woodlands. Removal experiments demonstrated that the species did compete for space, but the interaction was comparatively weak and did not lead to habitat exclusion (Montgomery, 1981). A review by Montgomery and Bell (1981) suggested that when *A. sylvaticus* shares woodland with *C. glareolus*, the former has no discernible preference for any cover type, whereas the latter is restricted to dense vegetation close to the ground. However, in the absence of this potential competitor, captures of *A. sylvaticus* are concentrated in these vegetation patches which provide ground cover. Greenwood (1978) showed that *A. sylvaticus* was nocturnal in the field with a single peak of activity, and *C. glareolus* was predominantly diurnal with peaks of activity at dawn and dusk. However, in the laboratory there was little indication of a diel preference. Hence different activity patterns in nature may result from interspecific interactions. In a Polish alder forest, *Apodemus agrarius* was the inferior competitor with respect to *A. flavicollis* and *C. glareolus* (Gliwicz, 1981). These two species negatively affected the density, the survival of offspring, the survival of older individuals, and reproduction of *A. agrarius*. Gliwicz hypothesized that the negative interactions within the community are caused by competition for food, especially in the midsummer period, when densities of animal food and of the seeds of the previous year have decreased.

Dueser and Shugart (1979) used discriminant analysis to define the microhabitats of four small mammal species in a second-growth mesic forest (Tennessee, U.S.A.) in terms of eight measures of physical habitat structure. They concluded that *Peromyscus leucopus* is an abundant generalist, well adapted to the habitat as a whole, and that *Ochrotomys nuttalli*, the only other mouse, is a relatively rare specialist. *Tamias striatus* occupies an intermediate position between the former two species and exhibits intermediate abundance. *Blarina brevicauda*, an insectivore, is present only in low numbers. Using multiple regression analysis, Dueser and Hallett (1980) estimated the effects of habitat selection and competition on the local distribution of these species during three seasons, and came to the conclusion that competition was pervasive among these species, the competitive ability and habitat selectivity both increasing in the order *Peromyscus–Tamias–Ochrotomys*.

Saprophages and microphytophages

"Decomposer" populations as a whole may be limited by the food supply (input of litter), by the spatial pattern of microhabitats, or by ecoclimatic factors. Wallwork (1976) found indications that the first situation is prevalent in saprophagous and

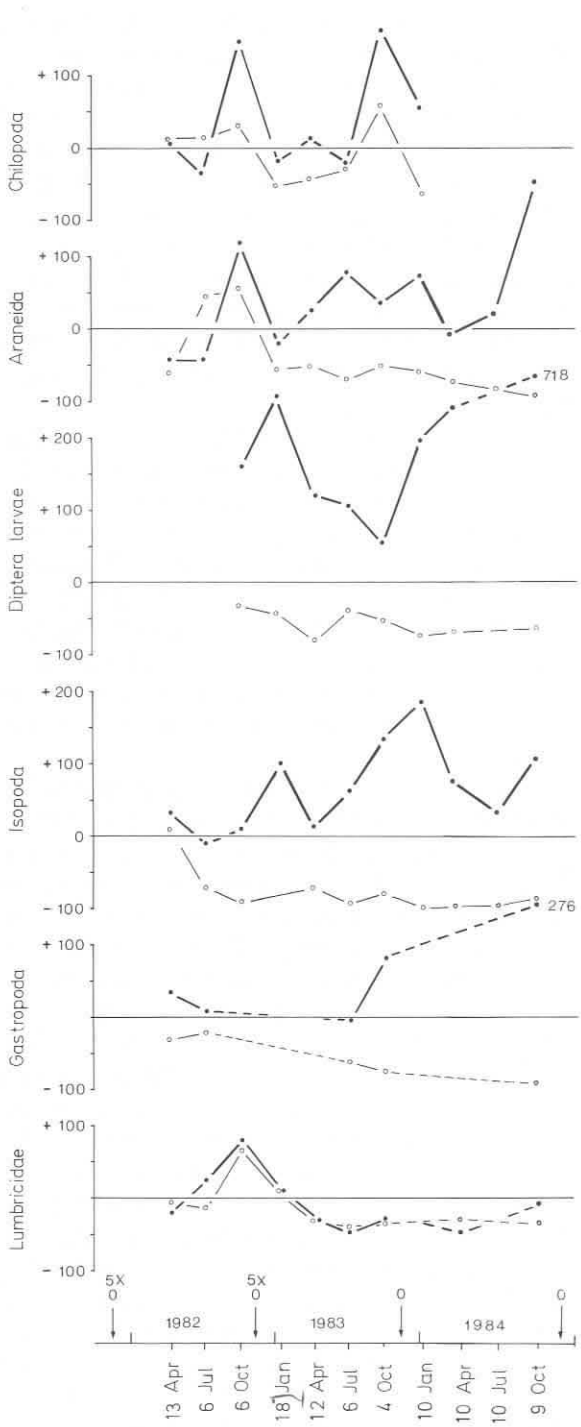


Fig. 6.16. Abundance of soil and litter fauna groups in experimental plots without canopy leaf-litter input (0) and with fivefold litter input (5×) in a beech-wood on limestone (Göttinger Wald). Thin line: density on plots without litter input, thick line: density on plots with fivefold litter input, as % increase or decrease in relation to control plots with normal litter input. Based on unpublished results from M. Judas (Lumbricidae), M. Corsmann (Gastropoda), R. Strüve-Kusenberg (Isopoda), K. Hövemeyer (Diptera), G. Stippich (Araneida) and T. Poser (Chilopoda).

microphytophagous animal populations of soil and litter. Joosse (1975) observed that Collembola are often "hungry" in the field. Miller (1974) hypothesized that the non-accumulation of litter with time in deciduous woodland is circumstantial evidence that litter may be a limited resource. Limitation may be due to the unpalatability of apparently abundant types of leaf litter, and later due to the consumption of the majority of the litter. It is, of course, possible that saprophages are limited by other factors, such as predators or ecoclimate, and that litter is a limiting resource for microfloral populations, which are the main decomposers on the forest floor (see Chapter 9).

Anderson and Healey (1972) have put forward three hypotheses to explain coexistence and the high degree of diversity in soil microarthropods: (1) There is an excess of food. These populations are being regulated below the level of their resources either by predation, climate or some other environmental factors; (2) there exist some undetected differences in resource utilization; (3) there are undetected microhabitat differences between species. Probably all these factors interact to reduce the pressure of competition between the large number of species in the soil and litter, which, in most habitats, utilize resources which are superficially rather uniform (Anderson and Healey, 1972).

Experimental evidence of direct control of soil animal abundance by litter input is lacking. An experiment was designed to study the effect on the soil and litter community in a German beech-wood of different amounts of canopy leaf-litter input (Fig. 6.16). Some animal groups increased in abundance and/or biomass with increasing litter input, some groups were not affected, and some decreased in number. Most astonishingly, earthworm density and biomass did not increase in response to higher rates of litter input.

Macrofauna

Phillipson et al. (1976) found considerable ecological separation between earthworm species

in an English deciduous forest. Lumbricidae, judging from their gut contents (Piearce, 1978), have partly different food preferences. Satchell (1967) assumed intense competition between earthworm species; however, no clear experimental evidence exists. Competition was observed by Abbott (1980) in laboratory studies.

Jennings and Barkham (1979) made measurements of the vertical distribution of six species of slugs at night in a mixed deciduous woodland in England. Only two groups of species could be separated on this single niche dimension. The slugs fed largely on dead plant material. It appears that separation along the dimension of vertical feeding height is insufficient to separate most pairs of slug species. On windy nights during drought, or in subzero temperatures, the slugs remain low on the ground or beneath the litter layer, which means that in either case green food will be unavailable. Intraspecific competition for food may occur under these conditions.

Seven millipede species of a maple–oak forest in Illinois (U.S.A.) were at least partially segregated by preferring different microhabitats within the leaf litter or decaying wood (O'Neill, 1967). Miller (1974) analyzed the distribution pattern of the woodland floor species *Iulus scandinavius* and *Ophyiulus pilosus* in different British habitats. *O. pilosus* was found most often in the deeper litter accumulations at the foot of slopes. *I. scandinavicus* is found higher up in sparser litter, where conditions are thought to be drier. Several sites have mixed populations; here competition seems probable, but is not proven in the study. Gist and Crossley (1975) suggested that Diplopoda and snails with high demand for calcium in the litter may be competitors. If calcium is limited, the more mobile millipedes may outcompete the snails for calcium.

Mesofauna

Soil arthropods are a mixture of *r*- and *K*-strategists (Crossley, 1977). It is noteworthy that the soil microarthropod *r*-specialists (Collembola) and *K*-specialists (Oribatida) seemingly compete for the same resource, namely fungal hyphae.

Collembolan feeding may be prominent in periods of rapid mycelial growth, while oribatids may utilize senescent microflora (possibly with higher calcium concentrations). However, this seems to be a simplified view, since some of the oribatid and collembolan species are not exclusively microphytophagous (Petersen, 1980; Wallwork, 1983).

Is competition between species of the mesofauna not important (Anderson, 1977)? Anderson (1978b) conducted an elegant study establishing high-density populations of *Hermanniella granulata* and *Nothrus sylvestris* (Oribatida) in natural soil and litter microcosms in the laboratory. The two species in pure populations had overlapping niches, with differences in subhorizon and microhabitat occupation as well as food resource selection. In mixed populations, both species underwent significant niche shifts in their utilization of food and space. *H. granulata* moved into the litter layer, while the *N. sylvestris* population increased in the fermentation layer. A complex pattern of changes in microhabitat occupation and in the selection of major groups of food resources was also observed. The value of this study lies in the direct evidence of a competitive interaction as an interference phenomenon in these soil–animal populations.

Studies on Collembola are more descriptive. Kilbertus and Vannier (1979) made a qualitative and quantitative analysis of the diet in four Collembola species inhabiting the litter of a French hornbeam wood, using techniques such as electron microscopy and microgravimetry. The diet of *Tomocerus minor* seemed to be composed mainly of hyphae, as evidenced by the presence of abundant fungal walls in the gut. *Allacma fusca* also fed preferentially on fungi, but spores were digested, whereas hyphae appeared intact. *Orchesella villosa* fed mainly on algae. *O. cincta* ingested algae too, but only used a small part of their cytoplasmatic content. Part of the matter ingested by these two sympatric species was identical, but the degradation process was quite different. This hypothesis was confirmed by the abundance of bacteria in the faeces of *O. cincta*. These preliminary results indicate that the four Collembola species divide the food resources of a restricted, apparently homogeneous biotope. In a study of sympatric collembolan species, Anderson and Healey (1972) found that the more fungivorous *Tomocerus minor* and *T. longicornis* were mainly associated with the more compacted raw humus horizons with higher microbial activity, whereas

Orchesella flavescens was characteristically associated with the layer of uncompacted leaf litter and took less fungal food.

Microfauna

There are some studies on competition and coexistence in soil Protozoa. Four species of Acrasieae (*Dictyostelium mucoroides*, *D. purpureum*, *Polysphondylium pallidum*, *P. violaceum*.) coexist in forest soils (Horn, 1971). All are capable of feeding and reproducing on a wide variety of the bacteria in their habitat. One species always outcompeted the others when the four slime moulds were forced to compete on a single strain of bacteria. Probably, the "coarse-grained" nature of the food distribution allows the coexistence of these four species of Acrasieae in nature. Competition between slime moulds was also found by McQueen (1971a, b).

Zoophages

Available information suggests that predators and parasites on the floor of temperate deciduous forests often are food-limited (Wallwork, 1976). Pressure by predators surely is high in the vegetation layers, as exemplified by *Formica rufa*. Skinner and Whittaker (1981) found in an English limestone woodland that trees without ants have significantly higher populations of Lepidopteran larvae than do trees with ants. On the latter, an average of 1% of the leaf area had been removed by defoliators at the end of the season; without ants the total was nearly 8%.

Litter macrofauna

Carabidae are the most intensely studied group of litter macrofauna. Carabidae partition their food resources (Thiele, 1977; Hengeveld, 1980) and differ in seasonal and diurnal activity patterns (Thiele, 1977; Löser, 1980). Hengeveld (1980) assumed that the differences in food preference are an ancient trait and not a recent reaction of phylogenetically unrelated species to their environment. Hence it is difficult to assess the applicability of models of optimal diets. Den Boer (1980) analyzed the guild structure of carabid communities and the role of interspecific competition, using pitfall catches of 149 carabid species during 9 years in 73 different habitats. He proposed a "coexistence principle" instead of the "principle of competitive exclusion". He was able to show that congeneric species of the carabid fauna of a variety of habitats in The Netherlands coexisted more frequently than could be expected from a random distribution of the species over the habitat. Interaction groups of coexisting congeneric species did not die out more frequently than those of species belonging to different genera, not even in the course of a century. His conclusion was that taxonomically closely related carabid species were also ecologically closely related, and would thus more often than not be found coexisting in the same habitat. Thiele (1977) made laboratory competition experiments with pairs of carabid species and failed to show conclusive competitive effects.

A very thorough analysis of the niche pattern of predatory beetles in an English deciduous forest was made by Dennison and Hodkinson (1983a, 1984a–c). They gathered data for important niche parameters of the dominant 23 species (mostly Carabidae and Staphylinidae): namely, prey selection, diurnal activity rhythms, seasonal activity rhythms, population density and community composition. The data suggest that in general the level of niche overlap is low, and that the niches of the different species are well differentiated. When coupled with the low population density recorded this implies that competitive interactions between the species are few.

Schaefer (1983b, 1986) analyzed the whole predatory litter macrofauna in a German beech-wood: Araneida, Pseudoscorpionida, Opilionida, Chilopoda, Carabidae, Staphylinidae. A community matrix for these groups utilizing niche dimensions of food, and temporal and spatial distribution, revealed low niche overlap. Ranking of the individuals according to relative biomass lead to a clear sequence of the animals with decreasing biomass. These results may support the assumption that the macroarthropods divide their prey resources by size (Fig. 6.17).

Canopy parasitoids

In a German beech-wood more than 500 species of parasitoids live in the canopy, herb and litter–soil layer (Ulrich, 1987). The ratio of parasitoids to possible insect hosts was much higher in the crown than in litter and soil; more

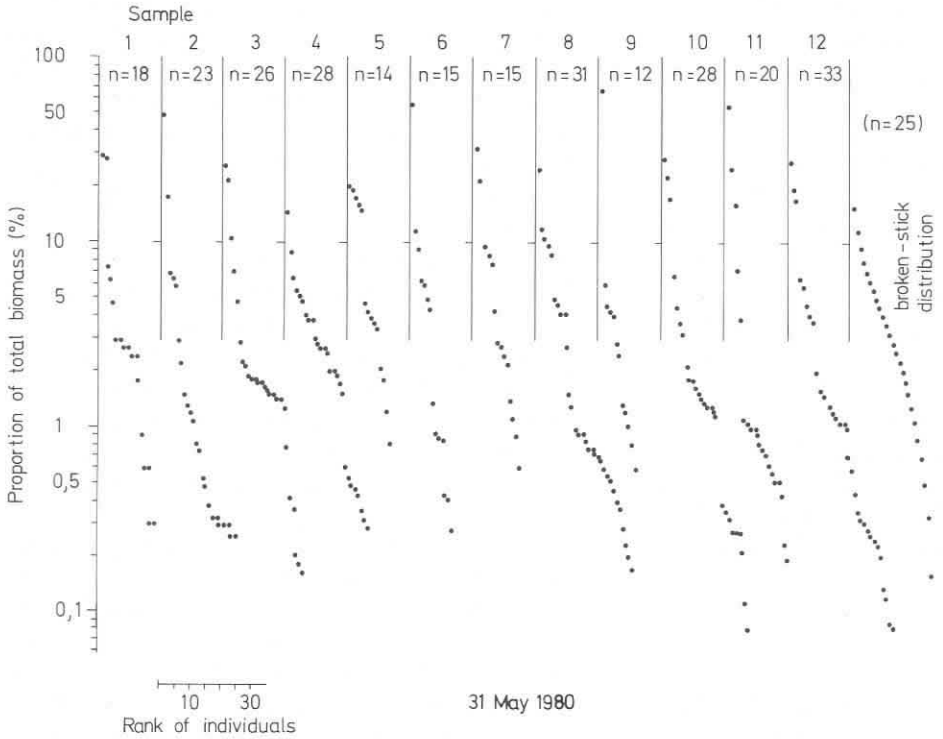


Fig. 6.17. Ranking of individuals of the predatory litter macrofauna in a beech-wood on limestone (Göttinger Wald) according to relative biomass. The data are based on 12 litter samples for 31 May 1980. n = number of individuals. For comparison the broken-stick distribution (for $n=25$) is given. Partly after Schaefer (1986).

parasitoids live in the crown than all other insects combined. Endophytophagous hosts (leaf miners and gall makers) supported more species of parasitoid wasps than ectophytophagous hosts (chewers and sap-feeders). The number of parasitoid species surpassed the number of endophytophagous host species.

Many parasitoids are monophagous or oligophagous; a more interesting problem is the partitioning of resources by polyphagous parasitoids. Among parasitoid communities of leaf miners (*Phyllonorycter*) and cynipid galls there are many polyphagous species (Askew, 1980). The coexistence of many cynipid species on oak may be at least partly explained by the partitioning of resources by polyphagous parasites attacking the galls; in contrast, polyphagous parasites in *Phyllonorycter* miners do not, in general, discriminate between primary hosts on the same pla and the number of coexisting *Phyllonor* parasitoid) species is restricted (Askew, 1980).

Most studies of parasitoid communities concentrate on those of canopy gall makers and leaf miners. There are few data on predation pressure by parasitoids in deciduous forests. Population studies, for instance for *Operophthera* (Geometridae), demonstrated that parasitoid populations may be a key factor in the regulation of host populations. The parasitization rate of the Lepidoptera in a German beech-wood was estimated to be >30% (Ulrich, 1987). Faeth and Simberloff (1981) demonstrated that parasitism of leaf miners by Hymenoptera decreased significantly with experimental isolation of oak host trees. However, the increase of larval survivorship of leaf miners on isolated oak trees was not followed by higher abundances in subsequent generations either within a season or in the following year, because leaf-mining populations, on small trees at least, are maintained by continual reimmigration.

vorous birds

Many insectivorous birds feed in the canopy. Some pick their food off leaves and twigs (such as

many warblers, Parulidae), others search the bark for insects (such as nuthatches, Sittidae, and woodpeckers, Picidae) and still other species capture insects on the wing (such as flycatchers, Tyrannidae). A separate group of birds (such as thrushes, Turdidae) feed on insects in the ground zone. Birds of temperate deciduous forests have the opportunity to be food specialists, because they are mobile and can migrate to other habitats when food resources become scarce (Richardson, 1977).

Many studies on ecological separation within this guild in temperate deciduous forests come to the conclusion that the species divide the resource axes of their niche, mainly horizontal and vertical distribution and food (Edington and Edington, 1972). Some examples are given, mainly for the European tits (*Parus* spp.) which are perhaps the best-studied group of birds as regards population ecology (for reviews see Lack, 1971; Perrins, 1979).

Hartley (1953) studied the feeding habits of five species of titmouse (great tit, *Parus major*; blue tit, *P. caeruleus*; coal tit, *P. ater*; marsh tit, *P. palustris*; long-tailed tit, *Aegithalos caudatus*) in English deciduous forests in the Midlands. The bird species differed in their distribution of foraging activities and preferences for tree species. This leads to ecological separation, which was found to disappear during periods of temporary superabundance of food. Lister (1980) reanalyzed data on foraging microhabitats of five species of *Parus* and the goldcrest (*Regulus regulus*) in two British woods. Spatial overlap was nearly complete during the summer months, then decreased during the fall and winter, and reached a minimum value in the early spring. Clearly competition for food plays a major role in reducing niche overlap. In an English mixed deciduous forest (Wytham Wood) there is interspecific competition between breeding blue and great tits (Minot, 1981). Breeding success of great tits, as measured by the mean fledgling weight of each chick in a brood, was negatively correlated with the density of blue tits. An area of woods from which all blue tit young were removed at hatching had significantly heavier broods of great tits when compared with the control area. Minot (1981) suggested that competition for insect food by breeding birds in temperate regions may be an important source of diffuse competition.

In a review, Perrins (1979) emphasized that British tits are segregated by habitat, choice of food, and/or nesting site. Alatalo (1982a), in a recent evaluation of the existing data, came to the conclusion that in European tits evidence for interspecific competition is already extensive; however, it is still difficult to draw firm conclusions about the importance of interspecific competition in structuring tit communities.

In a Finnish deciduous forest the insectivorous passerine flycatchers (*Muscicapa striata* and *Ficedula hypoleuca* and the redstart *Phoenicurus phoenicurus*) form a guild with a similar foraging strategy (Alatalo and Alatalo, 1979): they hawk insects from the air, but also from trees and the ground. A niche study analyzed the following resource axes: habitat, "macrosubstrate" (air, tree, ground), tree species, tree height, tree part and height in the air. Foraging sites overlapped considerably, but the species differed in the use of the tree macrosubstrate categories (Alatalo and Alatalo, 1979). In another paper, Alatalo (1982b) presented data on the foraging niches of 9 foliage-gleaning bird species in Finland (among them 4 *Parus* spp.). Tree part was the most important axis for niche separation, perhaps owing to its close association with body size. Overlap of foraging niches was lower in winter than in summer, perhaps to avoid interspecific competition for limited food resources in winter.

Wagner (1981) analyzed the guild structure of a foliage- and bark-gleaning guild of 15 species of insectivorous birds in a California oak woodland for two years. Seasonal differences in choices of plant type, perch size, and foraging heights were fewer than differences between years in the same season. Species most similar in foraging sites were distinct in bill size or behaviour, except for the chestnut-backed chickadee (*Parus rufescens*) and Hutton's vireo (*Vireo huttoni*). These two species are viewed as potential competitors.

In an eastern temperate deciduous forest (Tennessee, U.S.A.) insectivorous birds subdivide their habitat (Anderson et al., 1979). Bark-gleaning birds show a vertical stratification, whereas canopy feeders are active at different times of the day. Additionally, there are vertical behavioural differences: branch and foliage gleaning is concentrated between 6 and 20 m, while trunk gleaning is largely restricted between 6 and 10 m. Singing birds were most commonly observed between 6 and 12 m.

ORGANIZATION OF THE ECOSYSTEM AND FUNCTIONAL RELATIONSHIPS

According to Swift et al. (1979), an ecosystem is characterized by the integrated and largely self-maintained functioning of a diverse community of organisms within a range of physical environment. These authors relate an ecosystem to an area which is self-contained in terms of its primary production and nutrient cycling. My discussion mainly concerns the position of the animals in this system and functional interrelationships between the different constituent populations and trophic levels (Fig. 6.18) O'Neill and Reichle (1979) emphasized general system properties, such as total biomass, productivity and nutrient cycling, and minimized consideration of taxa. The influence of animals on ecosystem persistence through energy flow and nutrient cycling is considered in Chapter 9.

Major aspects of the forest animal community in an ecosystem context are population dynamics, population limitation and the food-web organisation. How are populations of different forest species limited and regulated? There is a large amount of literature on phyllophages: for instance, the aphids *Drepanosiphum platanoides* on sycamore and *Eucallipterus tiliae* on lime (Dixon, 1979) and the lepidopterans *Operophthera brumata* (Varley et al., 1973, Strong et al., 1984), *Oporinia autumnata* (Tenow, 1972), and *Malacosoma pluviale* (Wellington, 1960). Less studied are zoophages (for instance, tits: Perrins, 1979) and "saprophages" (for instance, Collembola, Joosse, 1975). Food and/or predators appear to be important density-dependent factors regulating population numbers.

Food webs

Interrelationships between trophic levels

Unfortunately, community-centred ecosystem studies on the dynamic relationship between the populations of different trophic levels are lacking.

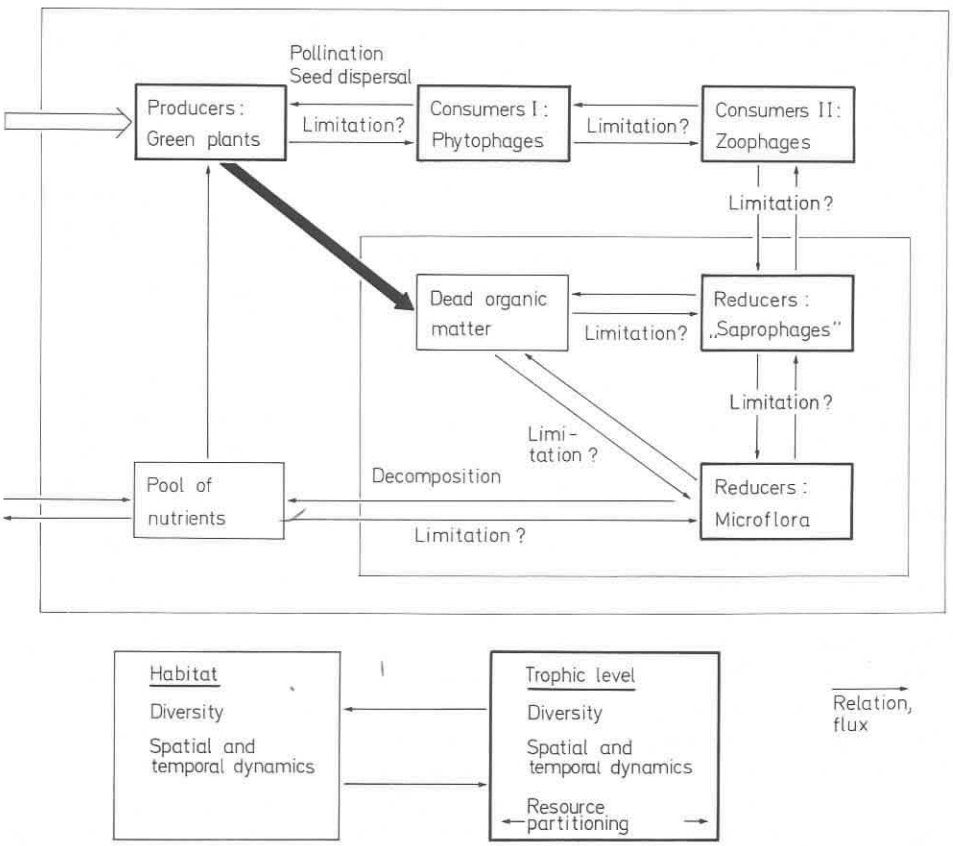


Fig. 6.18. A simplified graph of structural and functional relationships in a forest ecosystem.

Does scarcity of food regulate the dynamics of herbivorous insects? This may be possible; phytophages consume only about 1 to 10% of plant biomass (see Chapter 9); because of anti-herbivore defences not all that is green is palatable (Wiegert and Petersen, 1983). Strong et al. (1984), however, did not detect significant interspecific competitive interactions in contemporary communities of herbivorous insects. On the other hand, herbivores influence population dynamics of plants (by feeding, pollination, seed dispersal) and help to maintain plant species diversity.

Because of their high utilization rates, zoophagous populations may be regulated by limited energy (or nutrients) together with its temporal and/or spatial heterogeneity (Wiegert and Petersen, 1983). Grazing microphytophagous animals may be limited by the amount of available microbial biomass (Wallwork, 1976).

Input of dead organic matter

It can be hypothesized that litter production limits decomposer populations as a whole. Hence McBrayer et al. (1977) suggested that litter production determines microarthropod densities. However, Harding and Stuttard (1974) noted that microarthropod densities increase with latitude. Thus microarthropod densities seem to be correlated with standing crop of organic matter and not with litter production (Petersen and Luxton, 1982). According to Wiegert and Petersen (1983), those saprophages feeding on detritus, which is "highly unpredictable in space and time", can be regarded as energy-limited. But it is doubtful if many species are in this category.

Obviously, as part of ecosystem organization, there is a rather continuous input of dead organic matter which is available for the decomposer trophic level. It is interesting to note that ground vegetation is a major contributor to litter production, the temporal pattern of which is to some extent complementary to that of the tree stratum. Half or more of the ground-vegetation litter in a Danish beech-wood is produced in the first half of the season, most particularly the months of June and July (Hughes, 1975).

For arthropods there are similarities between the soil–litter and the above-ground plant subsystem (Mattson, 1977): (1) scarcity of nitrogen, and perhaps other elements like phosphorus and sodium; (2) an abundance of nearly indigestible substances: (3) pervasive presence of secondary plant compounds; (4) an abundance of microorganisms that are intimately associated with arthropod microhabitats, foods and bodies.

Stability and resilience

Energy and material flow are not sufficient for a complete analysis of an ecosystem, although they are exceptionally important forms of information. The resistance and resilience of an ecosystem is not explained by these data alone. Rather, the interactions between species, fuelled by energy and involving material transfers, may be of greater significance. However, the spatial–temporal features of such interactions are poorly understood, especially in the context of the whole system.

Some processes which contribute to these ecosystem properties, and in which animals are involved, appear to be feedback loops in population interactions, diversity and heterogeneity, use of the litter layer as shelter during stress periods, control of flux patterns (see Chapter 9).

Heterogeneity may appear in a variety of ways (O'Neill and Reichle, 1979): diversity of species, spatial heterogeneity (habitat diversity, patchiness and aggregations), or genetic heterogeneity within populations. Such heterogeneity is apparent in natural systems; it can be viewed in terms of redundancy in function and pattern. Redundancy is essential so that any single perturbation is unlikely to destroy all capability for performing a critical function.

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